

A CENOMANIAN FLORA FROM THE WINTON FORMATION, EROMANGA BASIN, QUEENSLAND, AUSTRALIA

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A middle Cretaceous (Cenomanian) fossil flora from the Winton Formation of central Queensland consists of six taxa of ferns, four conifers, one ginkgophyte, one pentoxylalean, and eight angiosperm leaf types. It is the oldest impression flora to contain abundant angiosperm leaves to date described in detail from Australia, and provides the first, direct, macrofossil evidence of the transition from gymnosperm- to angiosperm-dominated floras in Australia during the Cretaceous. The angiosperm leaves are mostly hamamelid types of probable fagaceous or betulaceous affinity, but precise relationships are unclear. The Winton angiosperm assemblages show some similarity to Late Cretaceous floras of New Zealand.

□ *Late Cretaceous, Cenomanian, Winton Formation, Eromanga Basin, palaeobotany, angiosperms, pteridophytes, conifers, ginkgophytes.*

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Lack of Australian Late Cretaceous macrofossil floras has long hindered understanding of the origins, diversification, and biogeography of early austral angiosperms and conifers. Earliest records of angiosperms in the Australian fossil record are rare occurrences of dispersed monosulcate pollen grains from the Barremian of the Eromanga Basin, southern Queensland (Burger, 1988) and the Barremian-Aptian or early Albian Koonwarra Fossil Bed, southeastern Victoria (Dettmann, 1986). It is not until the mid-Albian that the monosulcate pollen types become significant components of Australian palynofloras in terms of diversity or abundance; triaperturate pollen is first recorded in the middle Albian (Burger, 1988). The palynology and biostratigraphy of Australian Cretaceous strata are well documented (Dettmann & Playford, 1969; Burger, 1973, 1980, 1988; Stover & Evans, 1973; Playford et al., 1975; Morgan, 1980). Particular emphasis has been placed on the early angiosperm component of Australian Cretaceous pollen floras (e.g., Dettmann, 1973; Dettmann et al., 1992; Burger, 1990, 1993), and a progressive increase in the diversity of angiosperms beginning at about the Aptian and continuing through the Late Cretaceous is well documented. Although the systematic affinities of the suite of pollen taxa that account for this initial diversity are mostly unknown, they are morphologically similar to the pollen found in contemporaneous sediments elsewhere in the world and have been ascribed to the same form-genera and often species. Toward the end of the

Cretaceous the unique Gondwanan component of the extant Australian angiosperm flora is recognizable (*Nothofagus*, Proteaceae, Winteraceae, Epacridaceae). A similar palynostratigraphic sequence occurs in New Zealand (Couper, 1953, 1960; Raine, 1984) and Antarctica (Dettmann & Thomson, 1987; Dettmann 1989).

Owing to the paucity of outcropping Late Cretaceous sediments in Australia, reports of Australian Cretaceous angiosperm leaf remains are far less numerous and informative. Medwell (1954b) and Douglas (1969) discussed several unidentified angiosperm leaf and cuticle types from the latest Early Cretaceous of western Victoria, and Taylor & Hickey (1990) reported on a small, magnoliid, angiospermous leaf from the Koonwarra Fossil Bed. Walkom (1919a) described and illustrated several leaves from the Albian Burrum and Styx Coal Measures of central Queensland. As a consequence, there is no comprehensive body of macrofossil evidence relating to the mid-Cretaceous diversification of angiosperms in Australia, the early development of the modern Australian flora, or the non-angiosperm floristic element that accompanied the change from gymnosperm-dominated Early Cretaceous floras to angiosperm-dominated Late Cretaceous and Tertiary floras. The flora described here from the Cenomanian Winton Formation is the first Australian Late Cretaceous leaf megafloora to be recorded in detail.

GEOLOGICAL SETTING

The Winton Formation extends over a broad area of southwestern Queensland, northeastern South Australia and northwestern New South Wales. It consists largely of siltstones and volcanolithic sandstones with minor mudstones and coals (Senior et al., 1978), reaching thicknesses of around 1200m in central parts of the basin (Moore & Pitt, 1984). The formation is the uppermost unit of the Manuka Subgroup within the Rolling Downs Group and incorporates the youngest Cretaceous strata of the Eromanga Basin. Fielding (1992) recognized three major facies associations within the unit, representing major channel, flood basin, and mire environments. Fielding (1992) interpreted the Winton Formation succession as an alluvial plain deposit generated by fluvial systems draining inwardly towards the basin depocentres where more persistent lacustrine conditions may have existed as evidenced by the presence of a range of fossilized dinoflagellate taxa at least in lower parts of the formation (Morgan, 1980).

The Winton Formation conformably overlies shallow marine and coastal deposits of the Mackunda Formation dated as Albian on the basis of invertebrate and palynomorph assemblages (Day et al., 1983). The Winton Formation has yielded spore-pollen assemblages belonging to the *Phimopollenites pannosus* or succeeding *Appendicisporites distocariniatus* zone of probable late Albian to Cenomanian age (Dettmann & Playford, 1969; Burger, 1970; Morgan, 1980; Helby et al., 1987). Moore & Pitt (1984), on the basis of unpublished palynological data suggested that the uppermost beds of this formation in central parts of the basin may have been deposited in the late Cenomanian or early Turonian. The Winton Formation also contains freshwater bivalves, insects, vertebrate body fossils, and dinosaur trackways of limited biostratigraphic utility (Dettmann et al., 1992).

The Winton Formation is disconformably overlain by Late Palaeocene to Eocene fluvial sediments of the Eyre Formation and regionally equivalent units (Day et al., 1983). These strata have been affected by several phases of duricrust development during the Palaeogene and Neogene. Low topographic relief, deep weathering, and duricrust cover commonly make distinction of the Winton Formation from overlying Palaeogene sediments difficult in isolated exposures. The plant assemblages described here probably derive from the Winton Formation

based on lithological criteria and the presence of typical Cretaceous plant groups (phylopteroid ferns, *Taeniopteris*, and ginkgoaleans). The macrofossil-bearing samples obtained from outcrop are too oxidized for palynological investigation.

MATERIALS AND METHODS

Plant fossils described here come from several outcrop localities in the Winton-Longreach district of central Queensland (Fig. 1). Illustrated specimens are lodged with the Queensland Museum (bearing catalogue numbers prefixed 'QMF') or the National Museum of Victoria (specimens prefixed 'NMVP'). Queensland Museum fossil locality numbers are prefixed 'L'. Some of the material was collected by Queensland Museum staff who endeavoured to obtain representative examples of the range of taxa from each locality. Other material was contributed by local landowners and opal miners for which only generalized locality details are available. Material from the following localities was investigated:

L165 - Western side of Tully Range (Brighton Downs 1:250 000 map), 23°02'S 142°23'E.

L224 - Cork Station (Brighton Downs 1:250 000 map); 23°01'S 142°24'E.

L406 - 6 km northwest of Whyrallah Homestead (Mackunda 1:250 000 map); 22°43'S 142°21'E.

L552 - New Year Creek, southeast of Mayneside, south-southwest of Winton; latitude and longitude uncertain.

L717 - 2 km west of Dalkeith Homestead, south of Winton; 23°31'S 143°11'E.

QMF17458 - Conway's Claim, near Opalton, south of Winton; latitude and longitude uncertain.

Plant fossils are preserved as impressions in buff, pale yellow, dark brown, or pink, siltstones or fine-grained lithic sandstones. Small cross-laminae and parallel laminae are evident in the host rocks and together with the relatively undamaged leaf remains and numerous slender invertebrate (?oligochaete) trails, they suggest relatively low energy, lacustrine, depositional environments. Many impressions are coated by a thin film of iron-oxides that occasionally shows indistinct epidermal imprints, but no organic matter is preserved. Cuticular features could not be discerned.

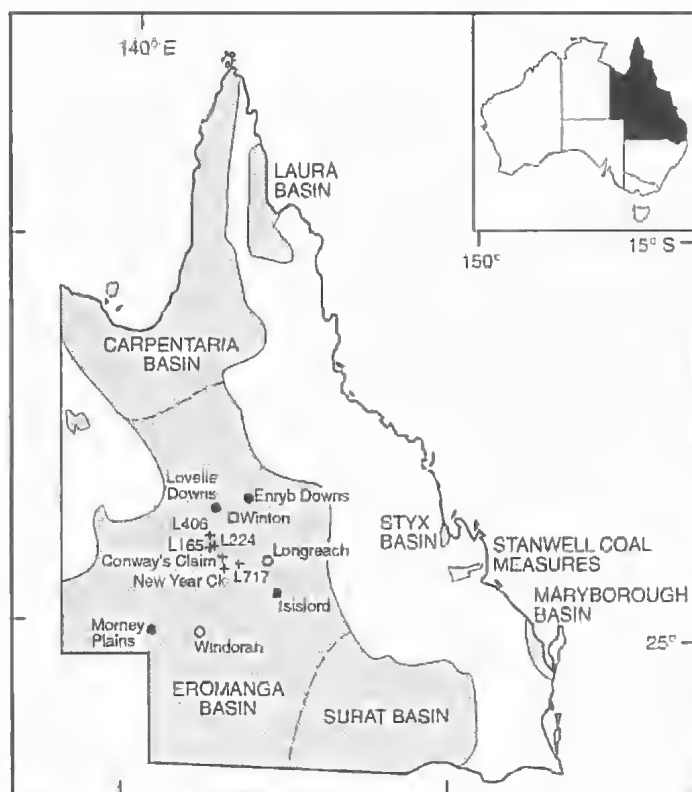


FIG. 1. Map of Queensland showing the distribution of Cretaceous sedimentary basins, selected towns (open circles), fossil localities studied here (crosses), and localities discussed in previous studies (closed circles).

PREVIOUS STUDIES OF WINTON FORMATION PLANT FOSSILS

Bose (1955) described equisetalean nodal diaphragms (*Equisetites* sp.), araucarian foliage-bearing shoots (*Araucaria* cf. *fletcheri* Selling, *Araucaria* sp.), bark impressions, and detached taxodiaceous foliage-bearing twigs and cones (*Athrotaxis australis* and *A. selligii* respectively) from Portland Downs Station, 25 km northwest of Isisford, central Queensland (Fig. 1). Bose (1955) proposed an (?)Oligocene age for the assemblage based on limited stratigraphic information. Bose's (1955) assemblage appears to contain several elements in common with the material described below and with that illustrated by Peters & Christophel (1978). More recent geological mapping indicates that the Winton Formation outcrops extensively through the Isisford area (Day et al., 1983) and is likely to be the source of Bose's material.

Whitehouse (1955) indicated the presence of *Protophylocladus*, *Nathorstia*, and dicotyledonous leaves in the Winton Formation but these determinations were not substantiated by descriptions or illustrations.

White (1966) noted the presence of araucariaceous foliage (which she referred to *Pagiophyllum peregrinum* Lindley & Hutton) from near the base of the Winton Formation at a locality approximately 11.2 km southeast of Enryb Downs Homestead, Winton district (Fig. 1). She also recognized linear, parallel-veined, possible cycadophyte pinnules from the same locality. White's (1966) specimens were not figured. She suggested a Jurassic or Lower Cretaceous age for this material.

White (1974) illustrated a slab of ferruginous sandstone from the Winton Formation, 5 km east of Morney Plains Homestead (west of Windorah: Fig. 1). The slab bears a large angiosperm leaf (which White referred to *Artocarpidium stuartii* Ettingshausen) and linear, striate, plant fragments (assigned to *Podozamites* sp. and *Equisetites* sp.). She also recorded the presence on another slab of a small conifer twig ascribed to *Pagiophyllum peregrinum*, and regarded the assemblage as Late Cretaceous in age.

Peters & Christophel (1978) described permineralized taxodiaceous cones (*Austrosequoia wintonensis*) from Lovell Downs Station (22°12'00"S 142°31'30"E), approximately 50 km northwest of Winton (Fig. 1). This locality also yields siliceous permineralized remains of various ferns, conifers, and angiosperms (Peters & Christophel, 1978) several of which appear to show surface morphological features identical to species here described from impressions. A range of plant remains from this assemblage was described by Peters (1985). Large collections of Winton Formation permineralized remains held by the Queensland Museum offer the potential for greater insights into the anatomy of plants in these austral early angiosperm floras.

Dettmann et al. (1992) illustrated a branched, foliage-bearing, araucarian twig and a cluster of araucarian cone scales from the Winton Forma-

tion of Whyrallah Station, Winton district, in their review of the Australian Cretaceous biota and terrestrial environments.

SYSTEMATIC PALAEOBOTANY

Phylum PTERIDOPHYTA
Class FILICOPSIDA
Order FILICALES
Family ?OSMUNDACEAE
Phyllopteroides Medwell, 1954

Phyllopteroides macclymontae sp. nov.,
(Figs 2A-D, 3A-H)

MATERIAL EXAMINED

HOLOTYPE: L717: QMF32543.

PARATYPES: L717: QMF32503, QMF32514, QMF32520, QMF32527, QMF32533, QMF32544, QMF32545, QMF32567, QMF32574, QMF32594-5, QMF32618, QMF32619, QMF32621, QMF32624, QMF32625, QMF32628-30.

ETYMOLOGY

For Mrs. Mary McClymont of Dalkieth Station who brought the plant fossil locality L717 to the attention of the Queensland Museum.

DIAGNOSIS

Narrow ovate to lanceolate pinnules, base cuneate acute to cuneate obtuse, apex pointed acute, margin serrulate or rarely lobed with 1-2 veins per marginal tooth. Rachilla slender, persistent, giving off regular once or twice dichotomous straight or gently curved lateral veins in subopposite to alternate arrangement at 20°-50°, rarely arching in outer lamina to 70°.

DESCRIPTION

Detached pinnules <39mm long, <18mm wide. Pinnules narrow ovate to lanceolate, base cuneate acute to cuneate obtuse (Fig. 3A,C,E-H), apex pointed acute, margin serrulate (dentation depth <0.5mm; 10-15 teeth per 10mm of margin) with 1-2 veins per marginal tooth (Fig. 3D,H). Margin divided into lobes in some specimens (Fig. 3B,G). Where present, lobes incorporate 2-5 ultimate veins and are separated by notches extending <1/3 distance to midrib, <2mm wide. Rachilla slender (<0.5mm wide), persistent, giving off regular once or twice dichotomous straight or gently curved lateral veins in subopposite to alternate arrangement at 20°-50° (more acute towards apex), rarely arching in outer lamina to 70° (Fig. 2A-D). Each lateral vein terminates in a distally flexed marginal cusp <1mm long, <1mm

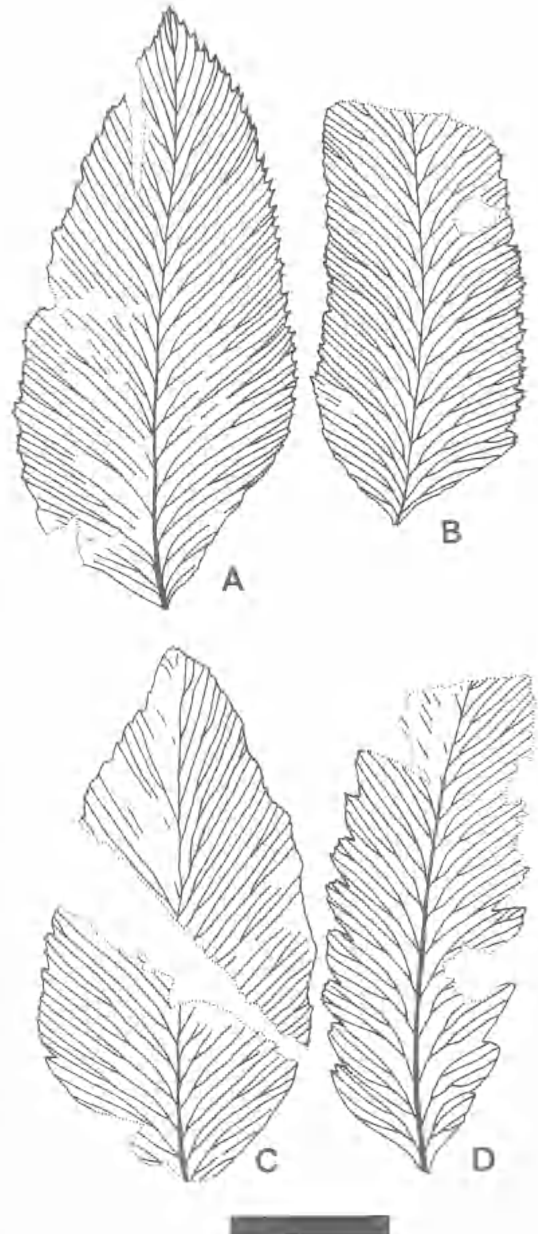


FIG. 2. Line drawings of *Phyllopteroides macclymontae* sp. nov. pinnules showing details of venation and lamina margin. A, QMF32543. B, QMF32594. C, QMF32597. D, QMF32595. All specimens from L717. Scale bar: 1 cm for all illustrations.

wide. Lateral vein density 12-23 per cm at margin. No fertile material available.

COMPARISON AND REMARKS

All preserved pinnae have been detached from the frond at the base of the lamina (no petiole is preserved). Etheridge (1893) established *Phyllopteris feistmanteli* for Late Cretaceous *Phyllopteroides* pinnules from the Cooper Creek area of South Australia and Early Cretaceous specimens from Stewart Creek in Queensland. Specimens from the latter site were transferred to *P. laevis* by Cantrill & Webb (1987). The Cooper Creek specimens are apparently lost (Cantrill & Webb, 1987) but may be coeval with the Winton material based on the distribution of exposed Late Cretaceous strata in the Cooper Creek area (Cowley & Freeman, 1993). The only illustrated Cooper Creek specimen (Etheridge, 1893: fig. 1) shows the basal portion of a leaf with an entire or slightly undulate margin unlike the Winton leaves. Further comparisons are not possible and the status of Etheridge's (1893) species remains uncertain.

Phyllopteroides macclymontae differs from *P. laevis* by its pointed acute apex (Fig. 3A,D) and commonly by its more acute secondary vein insertion angle. *Phyllopteroides laevis* is also a longer leaf, commonly reaching 70mm. *Phyllopteroides serrata* Cantrill & Webb 1987 is closely comparable to *P. macclymontae* on most morphological criteria but the latter appears to have a more regularly serrulate margin with typically one (rarely two) veins per marginal tooth rather than 2-3 veins per tooth in the former species. *Phyllopteroides macclymontae* also has a more distinctly acute apex.

Phyllopteroides lanceolata (Walkom) Medwell 1954 is distinguished from the Winton Formation pinnules by its lesser vein density, typically greater number of veins per marginal tooth (where these are present), and usually by its lesser marginal vein angle. *Phyllopteroides dentata* Medwell 1954 typically has more slender pinnules than *P. macclymontae*, together with a greater dentation depth, lesser concentration of marginal teeth, and greater number of marginal veins per tooth. Day (1964) reported *Phy-*

lopteroides leaves from the Bungil Formation (late Neocomian to early Aptian), Surat Basin, but provided no illustrations or descriptions of that material. However, Cantrill and Webb (1987) assigned Day's (1964) specimens to *P. laevis*. Western Australian Early Cretaceous *Phyllopteroides* pinnules (McLoughlin, in press) generally lack marginal teeth and are more slender than *P. macclymontae*. Cantrill & Webb (1987) indicated that the Queensland specimens assigned to *Phyllopteroides expansa* (Walkom) Medwell 1954b are probably referable to *Sphenopteris*. Leaves referred to *P. expansa* and *P. lanceolata* from the Lower Senonian of New Zealand (McQueen, 1956) are comparable to *P. lanceolata* and *P. serrata* on the basis of their lanceolate-elliptical shape and multi-veined marginal teeth. These features together with their more rounded pinnule apices differentiate the New Zealand specimens from *P. macclymontae*.

The evolutionary relationship between *P. macclymontae* (of Cenomanian age) and the lineages of eastern Australian Early Cretaceous *Phyllopteroides* species proposed by Cantrill & Webb (1987) is unclear. The reduced venation angle of *P. macclymontae* might suggest derivation through the *P. laevis* - *P. serrata* - *P. dentata* lineage. However, the relatively high venation and dentition density and few veins per marginal tooth might indicate an origin via the *P. laevis* - *P. serrata* - *P. lanceolata* lineage.

No sporangiate osmundaceous remains were found in the Winton Formation assemblages prohibiting comparisons with fertile remains assigned to *Cacumen expansa* Cantrill & Webb 1987 associated with *P. dentata* foliage in the Otway Basin.

Family GLEICHENIACEAE

Microphylopteris Arber, 1917

Microphylopteris sp. cf. *M. gleichenioides*
(Oldham & Morris) Walkom, 1919
(Fig. 4C,D)

MATERIAL EXAMINED
L552: QMF32477.

overleaf on p. 5

FIG. 3. *Phyllopteroides macclymontae* sp. nov. A, QMF32543, holotype showing spear-shaped pinnule, x 2. B, QMF32533, slender pinnule with lobed margin, x 2. C, QMF32574, small pinnule with slightly sinuous midrib, x 3. D, QMF32543, enlargement of holotype's apex showing one vein per marginal tooth, x 3. E, QMF32514, pinnule with broadly divergent basal lamina margins, x 3. F, QMF32597, hastate pinnule, x 3. G, QMF32595, pinnule with lobed margin, x 3. H, QMF32594, pinnule with finely toothed margin, x 3. All specimens from L717.

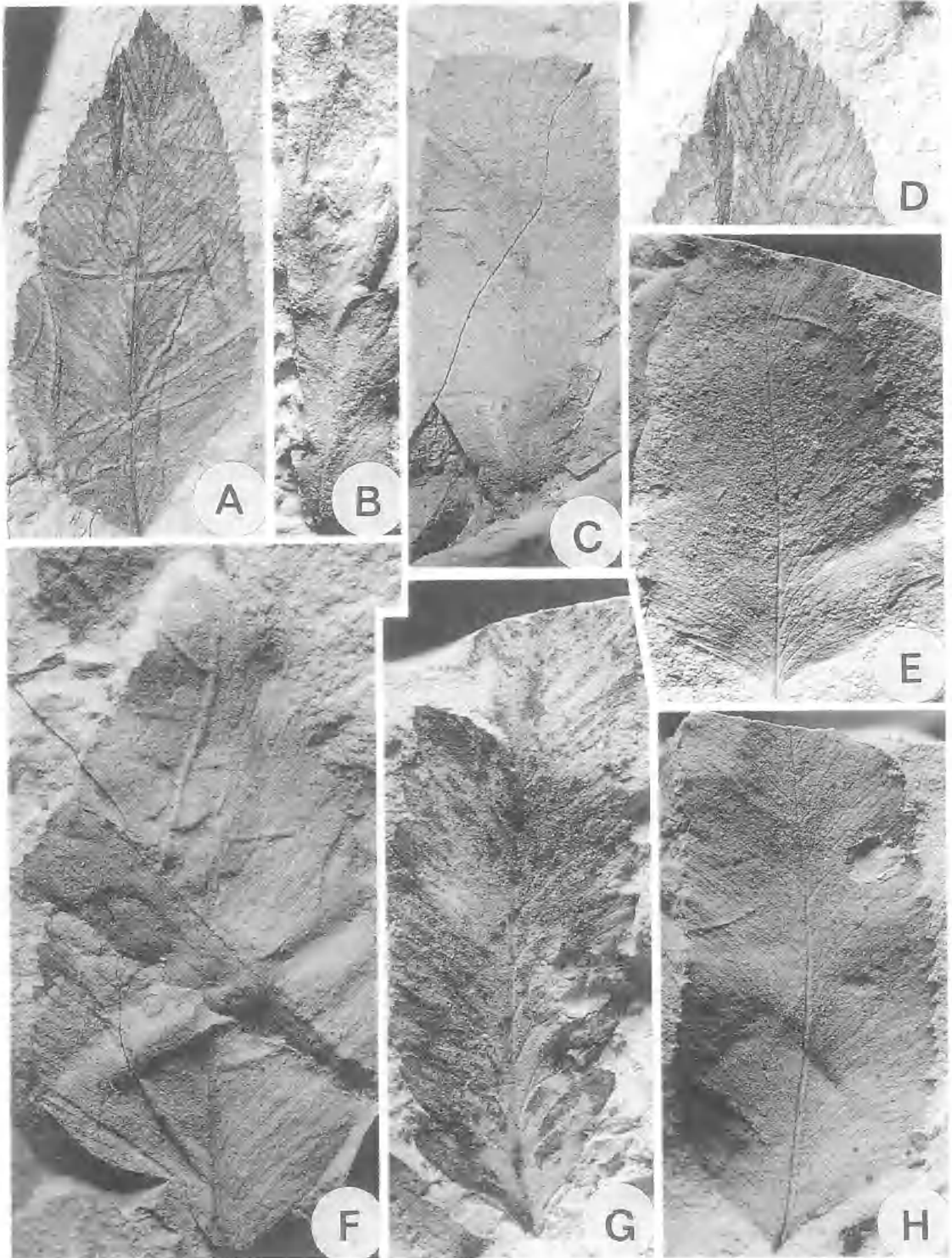


FIG. 3.

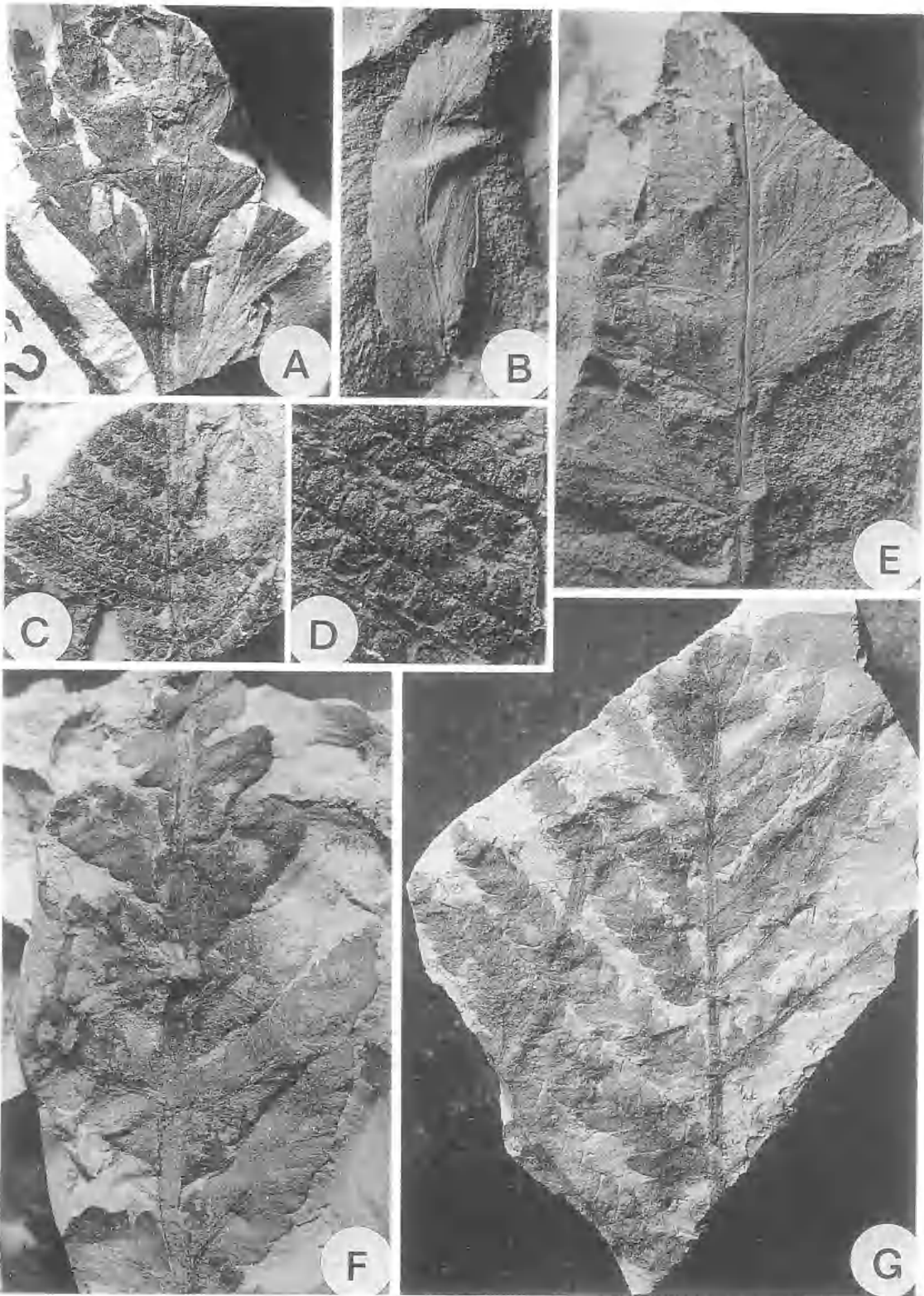


FIG. 4.

DESCRIPTION

Frond at least bipinnate, base and apex absent. Rachis slender (<1mm wide) expanded slightly where pinnae emerge. Pinnae opposite to subopposite, linear or gently falcate, bearing small elliptical, semi-circular, or oblong pinnules in subopposite to alternate arrangement. Pinnae reaching 2.5mm wide and >13mm long, depart rachis at 60°-70° (Fig. 4C). Pinnules decurrent, basiscopic margin strongly rounded (convex), apex rounded or truncate, acrosopic margin slightly convex, straight, or slightly concave, venation indistinct. Pinnules arched dorsoventrally (cup-shaped), reaching 1.5mm long and 1.2mm wide, departing rachilla at 60°-90° (Fig. 4D). Fertile material unavailable.

COMPARISON AND REMARKS

The single fragmentary specimen is insufficient for unequivocal specific identification. The numerous diminutive semi-circular to oblong cup-shaped pinnules with full basal attachment inserted on linear wide-angled pinnae (Fig. 4C,D) is suggestive of a gleicheniacean affinity. *Microphylopteris gleichenioides* (Oldham & Morris) Walkom 1919 occurs in several Australian Late Jurassic and Early Cretaceous assemblages (Gould, 1974; Walkom, 1919a, 1928; White, 1961b). This species is also common in Early Cretaceous Indian (Rajmahal and Jabalpur Formations) fossil suites (Seward & Sahai, 1920; Sah, 1965; Bose & Sah, 1968; Sukh-Dev, 1987). The Late Cretaceous Winton Formation specimen, although very incomplete, is closely comparable to *M. gleichenioides* on the basis of its small, slightly inclined, semi-circular pinnules, and linear pinnae arranged at high angles to the rachis.

Microphylopteris pectinata (Hector) Arber 1917 from the Jurassic and Lower Cretaceous of New Zealand and Australia (Arber, 1917; Walkom, 1919b) has substantially larger pinnae (>8cm) and pinnules (ca. 6mm long). *Gleichenites nanopinnatus* (Douglas) Drinnan & Chambers 1986 differs by its basally contracted, flabellate, and often lobed pinnules.

Gleichenia nordenskiöldii Heer 1874 of Sukh-Dev (1970) from the Lower Cretaceous (Jabalpur Formation) of India is distinguished from the Winton specimen by its expanded basal pinnule margins. The mid-Jurassic *Gleichenites juliensis* Herbst 1962 from Patagonia (Matildean beds) is distinguished by its proportionately more elongate pinnules. *Gleichenites sanmartinii* Halle emend. Herbst 1962 from the Aptian of Argentina (Kachaika Formation) has a superficially similar frond morphology to *M. sp. cf. M. gleichenioides* but differs by the contracted bases of its pinnules (Longobucco et al., 1985). However, Herbst's (1962) *G. sanmartinii* specimens from the Argentinian Early Cretaceous (Baqueró Formation) show pinnules with full basal attachment. They typically show pinnules arranged perpendicular to the rachilla but without the apical inclination evident in the Winton specimen. *Gleichenites vegagrandis* Herbst 1962 from the same Argentinian formation, however, does show apically inclined pinnules that are difficult to distinguish from the Queensland material. *Gleichenites cf. sanmartinii* of Arrondo & Petriella (1980) from the Early Jurassic of Argentina is also closely comparable to the Winton specimen although the details of pinnule attachments on the former are not clear.

Family UNCERTAIN

Cladophlebis Brongniart, 1849
Cladophlebis sp.
(Fig. 4F,G)

MATERIAL EXAMINED

L552: QMF32465, QMF32466, QMF32467. L717: QMF32626, QMF32627.

DESCRIPTION

Frond at least bipinnate. Base and apex absent in all specimens. Rachis prominent (3mm wide) tapering towards apex. Pinnae opposite to subopposite, lanceolate-lorate, reaching 65mm long, 18mm wide, inserted at 40°-70° to rachis. Pinnules falcate, apex acute, full basal attachment,

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FIG. 4. Fems. A, QMF32476, *Sphenopteris* sp. cf. *S. warragulensis* McCoy 1892, fragmentary frond, x 2, L552. B, QMF32558, indeterminate fern pinnule, x 3, L717. C, QMF32477, *Microphylopteris* sp. cf. *M. gleichenioides* (Oldham & Morris) Walkom 1919, fragmentary frond, x 2, L552. D, QMF32477, enlargement of pinnules in Fig. 4C, x 6, L552. E, QMF32505, *Sphenopteris* sp., fragment of frond with slender lanceolate pinnules, x 3, L717. F, QMF32465, *Cladophlebis* sp., apical portion of frond with variably lobed pinnules, x 2, L552. G, QMF32467, *Cladophlebis* sp., portion of large frond with opposite to sub-opposite pinnae and falcate pinnules, x 1, L552.

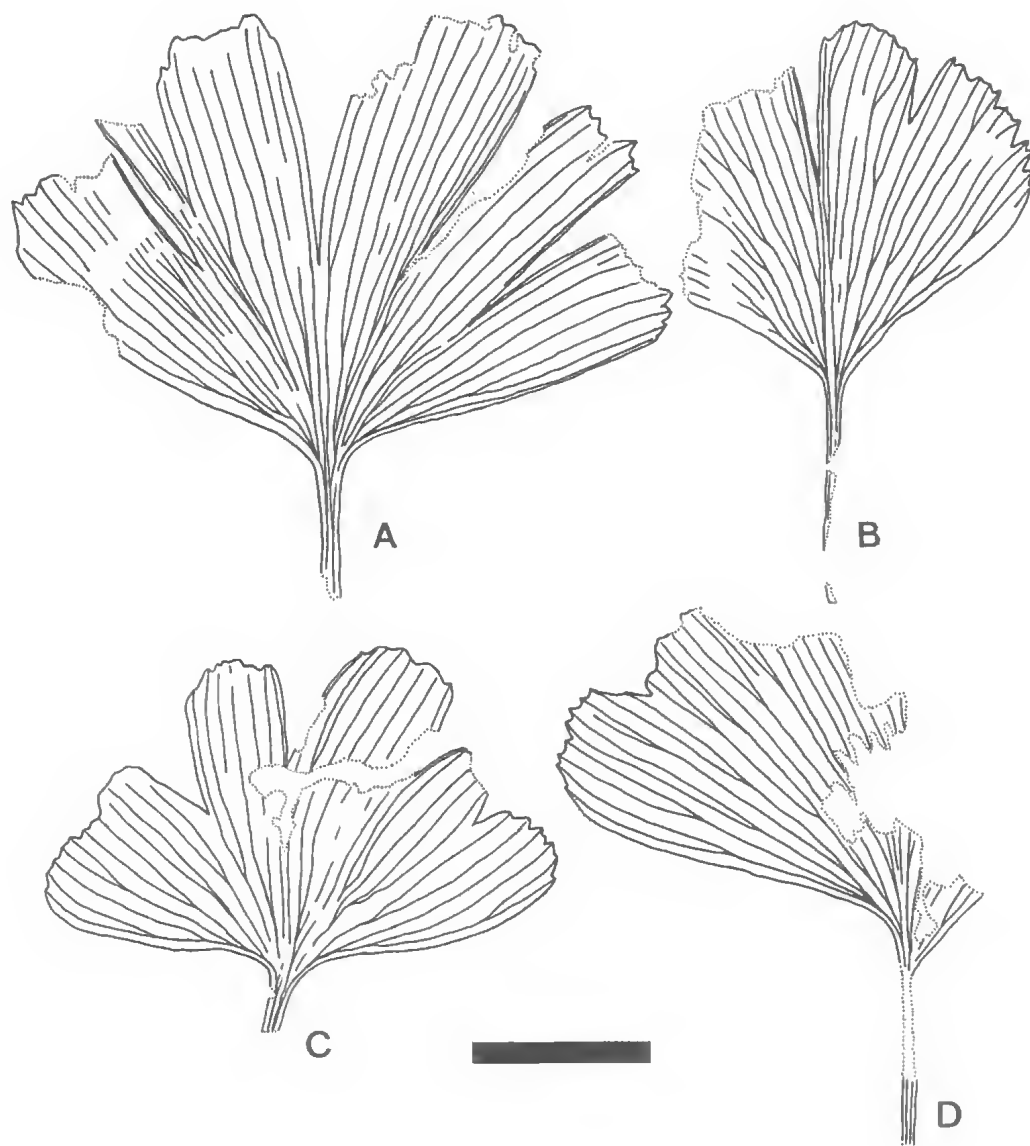


FIG. 5. Line drawings of *Ginkgo wintonensis* sp. nov. A, QMF32478. B, QMF32480. C, QMF32560. D, QMF32525. All specimens from L717. Scale bar: 1cm for all illustrations.

slightly decurrent and connected basally (pinnatisect). Pinnules reaching 22mm long, 6mm wide. Pinnule midribs persistent. Slightly sinuous alter-

nately inserted lateral veins may dichotomize once or twice before margin. Pinnules inserted at 40°-50° to rachilla. No fertile material available.

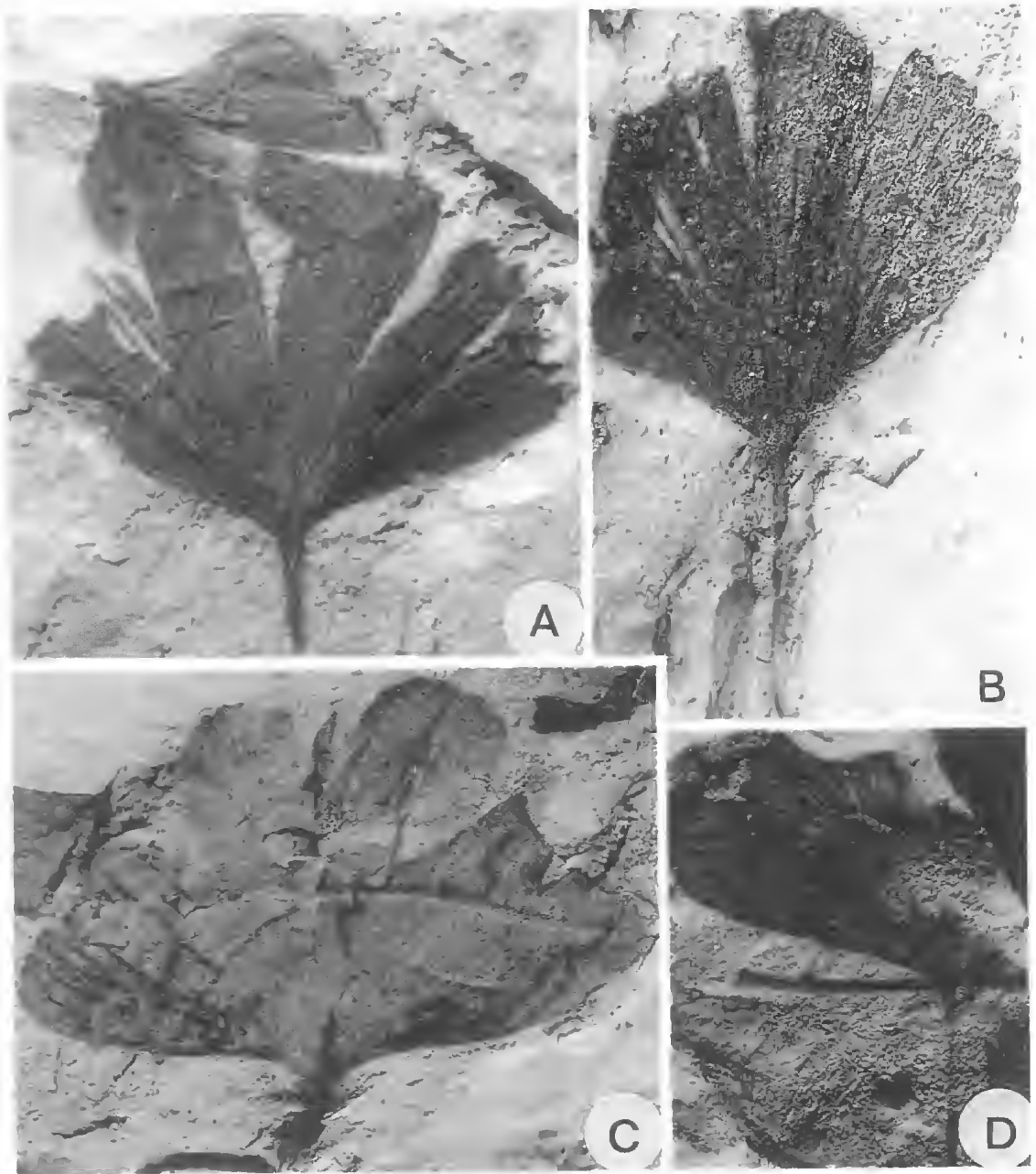


FIG. 6. *Ginkgo wintonensis* sp. nov. A, QMF32478, holotype showing moderately dissected lamina, x 2. B, QMF32480, leaf with minor dissection and long petiole, x 3. C, QMF32560, leaf with broadly divergent basal lamina margin and only minor distal dissection, x 3. D, QMF32525, fragment of leaf showing long petiole, x 2. All specimens from L717.

COMPARISON AND REMARKS

The studied specimens show differing pinna and pinnule shapes according to their position on the parent frond (Fig. 4F,G). As a consequence, individual pinnae and pinnules are comparable to

a range of Mesozoic *Cladophlebis* species described from various Gondwanan provinces. Discovery of more complete fronds may prove some of these species to be synonymous. The Winton fronds are similar to the long-ranging Mesozoic

species *Cladophlebis australis* (Morris) Seward in their entire or gently lobed, falcate, acutely pointed pinnules although pinnules of the former are mostly shorter (Walkom, 1917, 1919a, b; Hill et al., 1966). The Victorian Early Cretaceous species *Cladophlebis bififormis* Drinnan & Chambers 1986 and *C. sp. cf. C. oblonga* Halle 1913 also have proportionately longer entire-margined pinnules.

Specimens assigned to *Coniopteris ?lobata* (Oldham) by McQueen (1956) from the New Zealand Upper Cretaceous show pinnule variation similar to that of the Winton fronds but the former typically have more rounded and lobed pinnule apices.

Amongst the Indian forms, *Cladophlebis sp.* differs from *C. srivastavae* Gupta 1955 by its substantially larger pinnules (Gupta, 1955). *Todites indicus* (Oldham & Morris) Bose & Sah 1968 fronds differ only in their more sharply pointed pinnules. No fertile fronds are available amongst the Winton specimens to permit comparison with the sporangiate pinnules of *T. indicus*. South African Early Cretaceous fronds assigned to *Cladophlebis* spp. A, B, and C (Anderson & Anderson, 1985) have pinnules with more rounded apices than the Winton specimens.

Family UNCERTAIN

Sphenopteris (Brongniart) Sternberg, 1825
Sphenopteris sp. cf. S. warragulensis
 McCoy, 1892
 (Fig. 4A)

MATERIAL EXAMINED
 L552: QMF32476.

DESCRIPTION

Frond at least bipinnate, base and apex absent. Rachis prominently grooved (on impression).

Pinnae lanceolate-linear, subopposite to alternate, reaching 30mm long, 6mm wide (Fig. 4A). Pinnae inserted on rachis at approximately 30°, straight or gently arched distally. Pinnules lanceolate, reaching 11mm long, 2mm wide, subopposite, decurrent basiscopic margins extending along rachilla to form a narrow wing, inserted on rachilla at 10°-30°. Pinnule midvein persistent, branching several times to produce 3-5 acute, generally unbranched, lateral veins which typically terminate in acute marginal cusps. Initial veins in pinnules catadromous. No fertile material available.

COMPARISON AND REMARKS

The studied specimen closely resembles *Sphenopteris warragulensis* McCoy 1892 from the Victorian Early Cretaceous (Drinnan & Chambers, 1986) although no fertile fronds are available for comparison. Some *S. warragulensis* specimens show a greater degree of pinna dissection than the Winton frond but considerable morphological variation was reported amongst the Victorian foliage fragments according to their original position on the parent frond (Drinnan & Chambers, 1986). *Sphenopteris flabellifolia* Tenison-Woods 1883 from the Maryborough Basin Lower Cretaceous also has markedly dissected lanceolate fronds and may be closely allied to both *S. warragulensis* and the Winton frond. *Sphenopteris travisi* Stirling 1900 and *Sphenopteris sp.* of Drinnan & Chambers (1986) from the Victorian Lower Cretaceous both differ from the Winton specimen by their substantially shorter and more ovate to elliptical pinnae. Similarly, *S. erecta* (Tenison-Woods) Walkom 1919 has proportionately shorter rhomboid pinnules than *S. sp. cf. S. warragulensis*.

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FIG. 7. *Araucaria sp. cf. A. mesozoica* Walkom 1918. A, QMF32542, robust twig with broad elliptical leaves, x 1, L717. B, QMF32572, slender twig with narrow lanceolate leaves, x 1, L717. C, QMF32578, longitudinally fractured mould of robust twig showing arched, spirally arranged, scale-like leaves, x 1, L406. D, QMF32484, slender twig with intermediate-sized lanceolate leaves, x 1, L717. E, F32488, slender twig with linear leaves twisted to lie in a common plane, x 1, L717.

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FIG. 8. A-C, *Araucarian microsporangiate cones*; D-F, *Araucaria sp. cf. A. mesozoica* Walkom 1918 foliage. A, QMF32598, arched cone with densely crowded microsporophylls, x 2, L717. B, QMF32499, cone with lax peltate or elongate rhomboid microsporophylls, x 2, L717. C, QMF32446, cone showing axis with spirally arranged microsporophyll scars, x 5; L406. D, QMF32535, broad leaf with attenuate apex, x 1, L717. E, QMF32442, robust axis showing spirally arranged, broad, lanceolate leaves with broadly elliptical attachments, x 1.5, L406. F, QMF32561, slender twig bearing two ranks of narrow lanceolate leaves, x 1.5, L717.

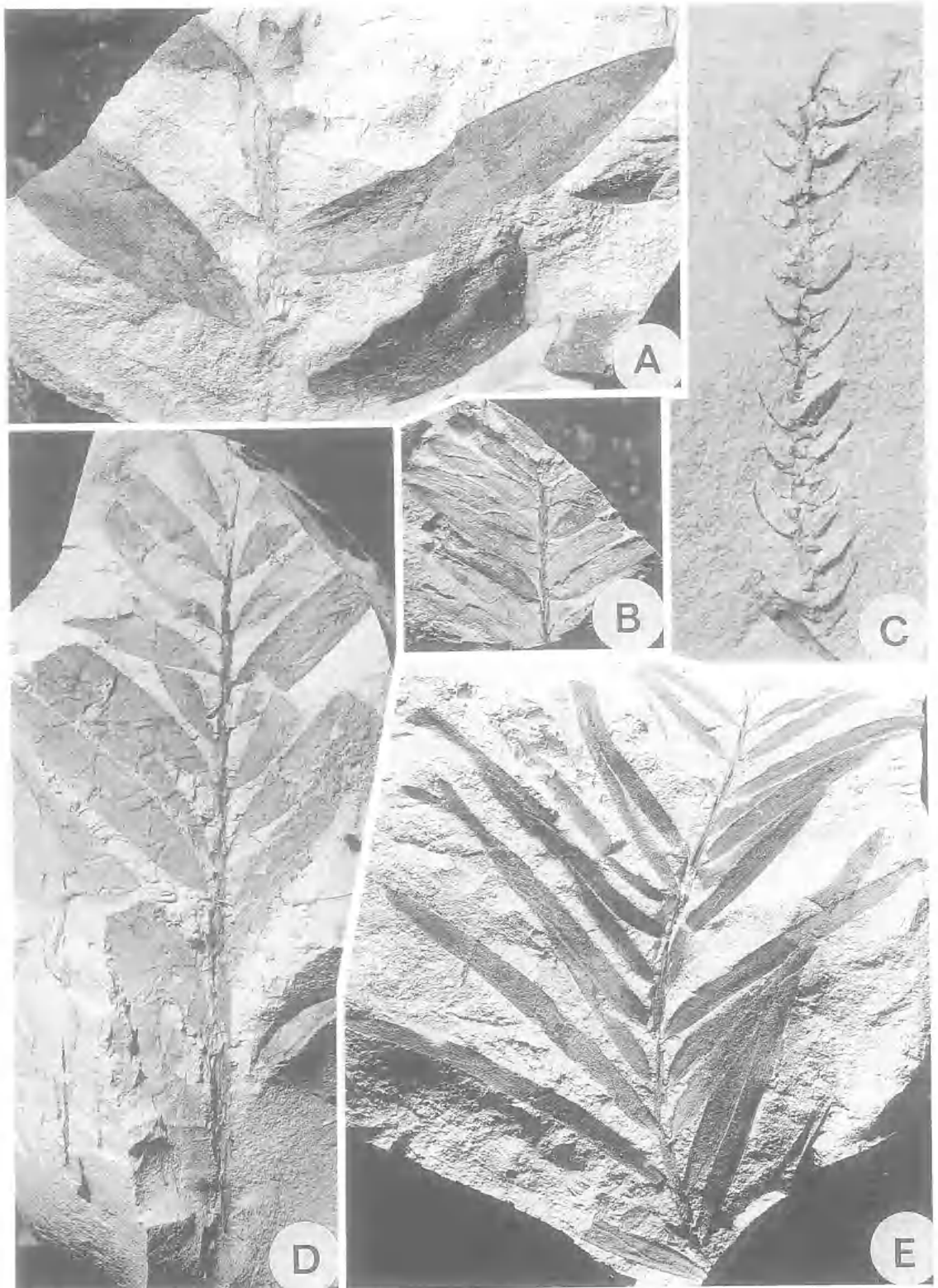


FIG. 7

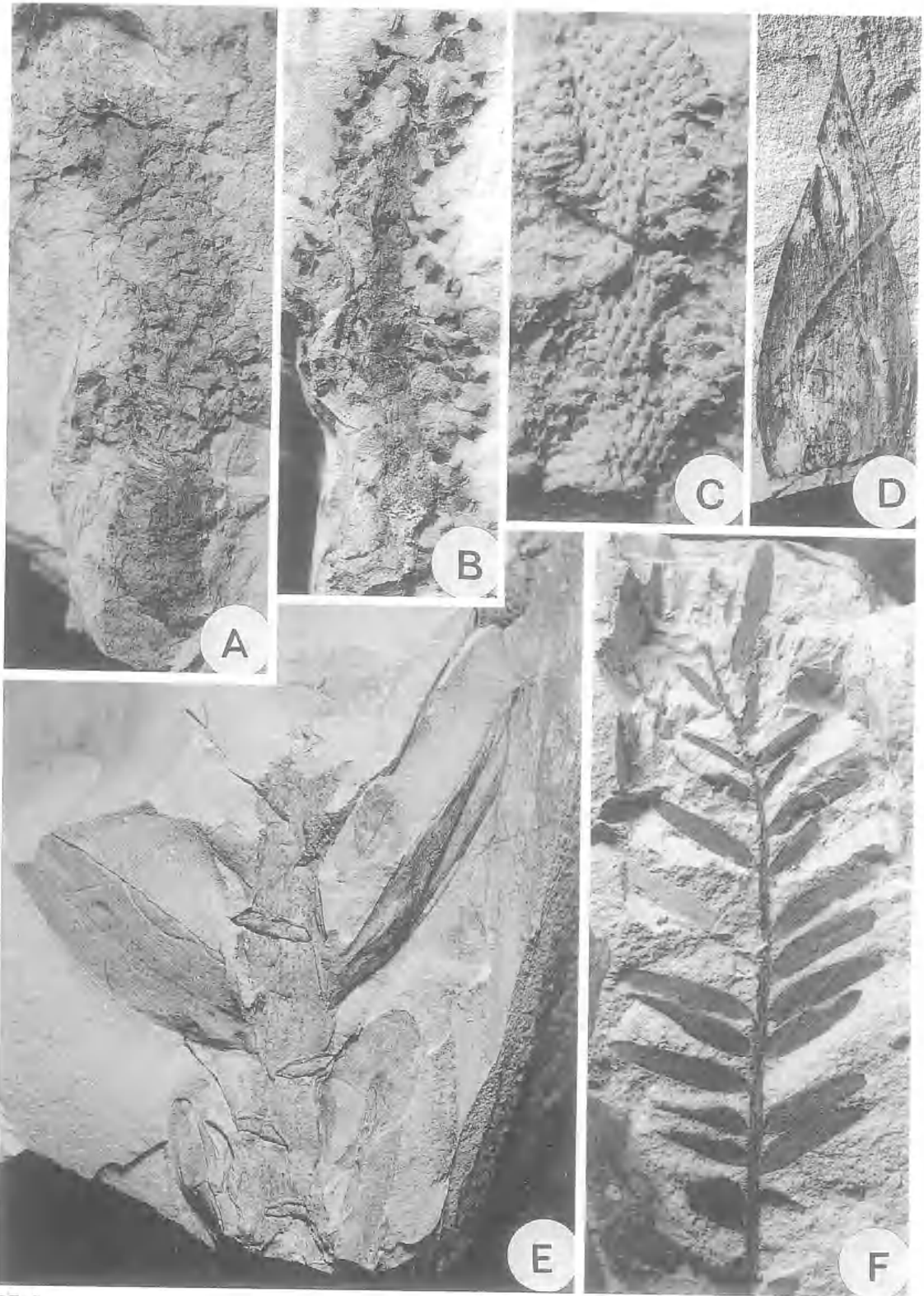
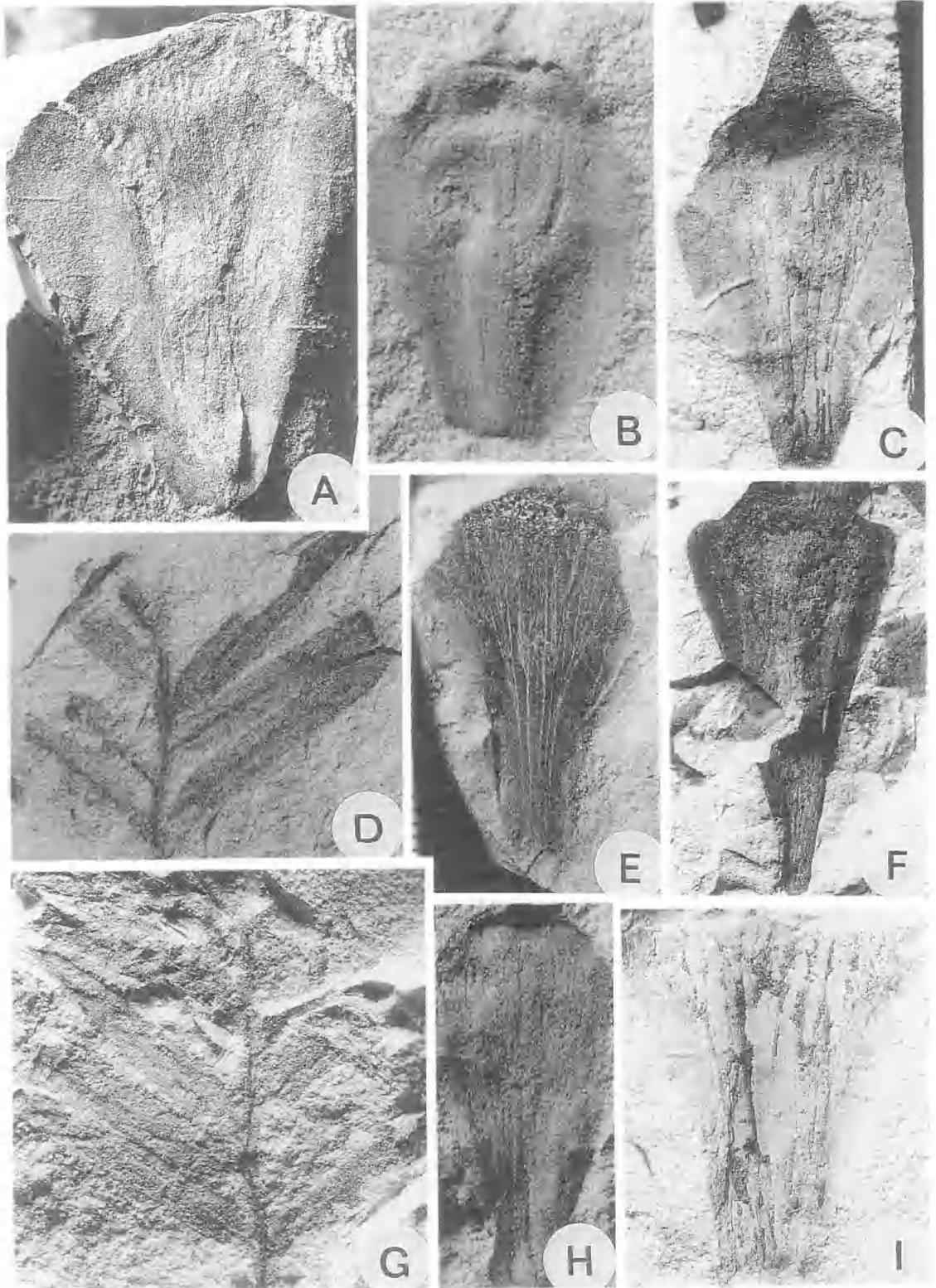


FIG. 8



***Sphenopteris* sp.**
(Fig. 4E)

MATERIAL EXAMINED
L717: QMF32505.

DESCRIPTION

Frond at least bipinnate, base and apex absent. Rachis prominently grooved (on impression), flanked by a slender (<0.5mm) wing. Pinnae ovate-elliptical, alternate, reaching >11mm long, 5mm wide. Pinnae inserted on rachis at 40°-60°, straight or gently arched distally. Pinnules linear-lanceolate, reaching 5mm long, 1mm wide, alternate, basiscopic margins decurrent, inserted on rachilla at 30°-40° (Fig. 4E). Pinnule midvein persistent?, lateral veins indistinct. Initial veins in pinnae catadromous. No fertile material available.

COMPARISON AND REMARKS

The single indistinct frond impression reveals little detail for comparison to previously illustrated ferns. The small pinnae dissected into slender pinnules (Fig. 4E) are reminiscent of several *Sphenopteris* species. The lanceolate pinnules of the studied specimen serve to differentiate it from the ovate, lobed pinnules of *S. travisi* Stirling 1900 and *Sphenopteris* sp. (Drinnan & Chambers, 1986) from the Victorian Early Cretaceous. White's (1961a) "*Stenopteris tripinnata* Walkom" from the Early Cretaceous Cronin Sandstone, Officer Basin, Western Australia, has pinnae dissected into linear pinnules although neither the Western Australian nor Winton Formation specimens are sufficiently complete or well-preserved to confirm synonymy. Zeba-Bano's (1980) *Sphenopteris* sp. B from the Early Cretaceous Jabalpur Formation, India, has slightly more elongate pinnae with slender obovate pinnules.

Indeterminate fern pinnule
(Fig. 4B)

MATERIAL EXAMINED
L717: QMF32558.

REMARKS

A single detached pinnule (Fig. 4B) from L717 may belong to a cladophleboid or sphenopterid fern. The pinnule is 18mm long, 6mm wide, lanceolate, with a slightly undulate margin. The pinnule midrib is sinuous, giving off sub-opposite to alternate, once-dichotomous, lateral veins at 20°-30°. Each lateral vein terminates in a short, blunt, marginal tooth. The pinnule shares characters with a number of Gondwanan *Cladophlebis* and *Sphenopteris* species but cannot be reliably assigned to either taxon owing to its incomplete preservation.

Phylum GINKGOPHYTA
Class GINKGOOPSIDA
Order GINKGOALES
Family GINKGOACEAE

Ginkgo Linnaeus, 1771
Ginkgo wintonensis sp. nov.
(Figs 5A-D, 6A-D)

MATERIAL EXAMINED

HOLOTYPE: L717: QMF32478.
PARATYPES: L717: QMF32479, QMF32480, QMF32496, QMF32525, QMF32537, QMF32560, QMF32561, QMF32620, QMF32622, QMF32623.

ETYMOLOGY

After the host formation.

DIAGNOSIS

Petiolate, flabellate leaves symmetrical about the petiolar axis. Distal lamina margin undulate to serrulate with one to five principle clefts incised to less than three fifths of the lamina width. Petiole <24mm long, <1mm wide, expanding into the lamina with a basal angle of 120°-180°. Venation gently divergent, dichotomizing <5 times chiefly in the proximal half of lamina, veins terminating in short marginal teeth.

DESCRIPTION

Leaf simple, petiolate, lamina 20-37mm wide, 17-30mm long. Leaves symmetrical about the petiolar axis. Petiole 12-24mm long, <1mm wide (Figs 5B,D; 6B,D). Lamina flabellate, dissected, basal angle 120°-180°. Major dissection, along

FIG. 9. A-C, E, F, H, I, Araucarian ovulate cone scales; D-G, cf. *Elatocladus plana* (Feistmantel) Seward 1918. A, QMF32482, broadly rounded scale, x 2, L717. B, QMF32447, broadly rounded scale with short spine, x 4, L406. C, QMF32540, scale with prominent venation and large apical spine, x 3, L717. D, QMF32515b, slender twig bearing oblong leaves with contracted bases, x 3, L717. E, F32502, scale with prominent dichotomous venation, x 2, L717. F, QMF32494, deltoid scale, x 2, L717. G, QMF32515a, counterpart to Fig 9D, x 3, L717. H, QMF32444, club-shaped scale, x 4, L406. I, QMF32563, scale with prominent venation, x 2, L717.

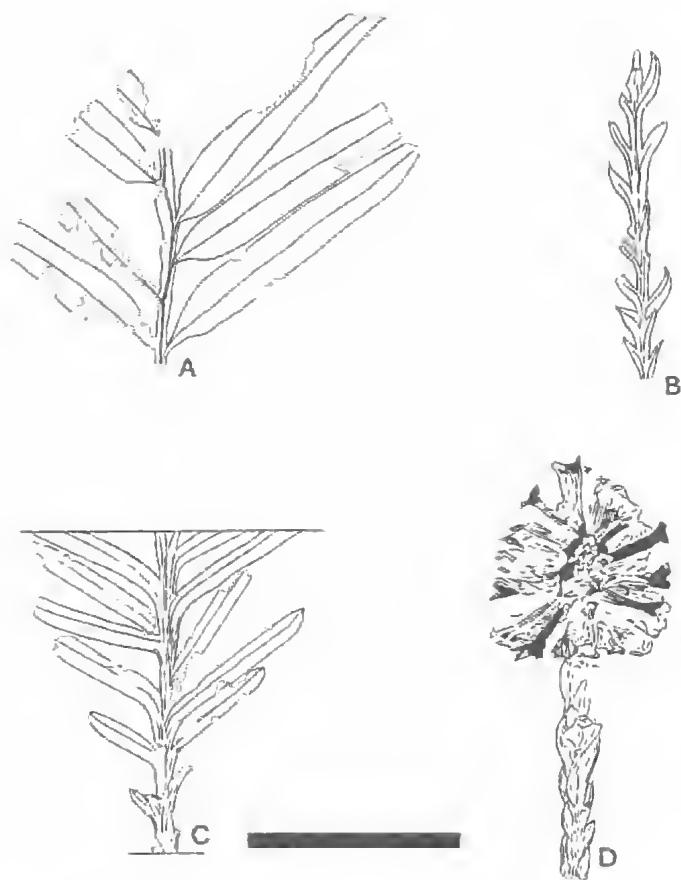


FIG. 10. Line drawings of selected Winton Formation conifer remains showing variation in leaf types. A, QMF32515b, cf. *Elatocladus plana* (Feistmantel) Seward 1918. B, QMF32491, cf. *Austrosequoia wintonensis* Peters & Christophel 1978, terminal portion of twig with arched scale-like leaves. C, QMF32564, Conifer sp. A. D, QMF32550, cf. *Austrosequoia wintonensis* Peters & Christophel 1978, axis with adpressed scale-like leaves and terminal cone. Scale bar: 1cm.

centre of leaf, $1/3 - 3/5$ width of lamina (Figs 5A,B; 6A,B). One to two dissections on either side of major dissection, incised $1/7 - 1/3$ width of lamina (Figs 5A-C; 6A-C). Venation gently divergent (Fig. 5A-D). Two veins emerge from petiole and bifurcate <5 times in proximal half of lamina, rarely bifurcating in outer lamina. Distal lamina margin undulate to serrulate, veins terminating in short (<1 mm) marginal teeth (Fig. 5B).

COMPARISON AND REMARKS

Fertile material and attached axes are unavailable for the Winton material. *Ginkgo australis* (McCoy) Drinnan & Chambers 1986 from the

Australian Early Cretaceous and the morphologically similar *Ginkgoites tigrensis* Archangelsky 1965 and *Ginkgoites ticoensis* Archangelsky 1965 from coeval South American strata (Archangelsky, 1965) differ from *Ginkgo wintonensis* sp. nov. by their generally larger lamina radius, more deeply dissected lamina, and narrower lamina segments. Walkom's (1918, 1919a) *Ginkgo digitata* (Brongniart) from the Maryborough Formation and Burrum Coal Measures, Maryborough Basin, is a smaller leaf form with a lesser degree of lamina dissection than *G. australis* but similar to *G. wintonensis*. However, Walkom (1919a) indicated that the Maryborough Basin specimens displayed a considerable range of leaf morphologies. Walkom's specimens show a lesser angle of basal lamina divergence from the petiole than do the Winton Formation specimens. The affinities of Walkom's (1918, 1919a) Maryborough Basin leaves will remain uncertain until better material is available.

Ginkgoites waarrensis Douglas 1965 from ?Cenomanian strata of Victoria was defined substantially on cuticular information as only a few incomplete leaves were available from bore core material. Douglas (1965) illustrated two macrofossil specimens at least one of which shows a petiolate leaf with a lamina dissected almost to its base. *Ginkgo wintonensis* leaves

from probable coeval Queensland strata show a lesser degree of lamina dissection but further comparisons are not possible owing to the lack of cuticular detail on the Winton specimens.

Fragmentary foliage assigned by Seward & Sahni (1920) to *Ginkgoites lobata* (Feistmantel) Seward and *Ginkgoites crassipes* (Feistmantel) Seward from the Indian Lower Cretaceous are similarly small leaves with comparable lamina dissection to *Ginkgo wintonensis* although the Indian forms show a lesser angle between the base of the lamina and the leaf midline. *Ginkgo rajmahalensis* (Sah & Jain) Zeba-Bano,

Maheshwari & Bose 1979 from the Indian Early Cretaceous incorporates substantially larger or more deeply dissected leaves than *G. wintonensis* (Sah, 1953; Mehta & Sud, 1953; Sah & Jain, 1965; Zeba-Bano et al., 1979). *Ginkgoites feistmantelii* Bose & Sukh Dev 1960, another Indian Early Cretaceous species, differs by its entire margin or very minor medial lamina cleft.

Ginkgoites waarrensis and *Ginkgo wintonensis* represent the youngest macrofossil examples yet recorded within Australia of the previously widespread and abundant ginkgoalean clade. Leaves of these Late Cretaceous ginkgoaleans are typically smaller than early Mesozoic Australian representatives but are otherwise similar in general morphology. Early Cretaceous Victorian and mid-Cretaceous Winton Formation ginkgoalean leaves were abscised whole (Drinnan & Chambers, 1986) and like the extant *Ginkgo biloba* were probably borne by deciduous plants. No major climatic changes have been invoked for the relatively high latitude Australian region during the Late Cretaceous (Dettmann et al., 1992). The causes for the extinction of ginkgoaleans from the Australian vegetation during the Late Cretaceous (together with pentoxylaleans, bennettitaleans, and equisetaleans) remain unclear although competition from the rapidly diversifying angiosperms may have played a role in their demise.

Phylum CONIFEROPHYTA
Class CONIFEROPSIDA
Order CONIFERALES
Family ARAUCARIACEAE

Araucaria Jussieu, 1789

Araucaria sp. cf. *A. mesozoica* Walkom, 1918
(Figs 7A-E, 8D-F)

Podozamites sp.; White, 1974: 2, fig. 4 (in part).

Equisetites sp.; White, 1974: 2, fig. 4 (in part).

Branchlet (*Araucariaceae*); Dettmann et al. 1992: fig. 15d.

MATERIAL EXAMINED

L406: QMF32440-3, QMF32576, QMF32578, QMF32599. L717: QMF32484, QMF32488, QMF32498, QMF32501, QMF32516, QMF32518, QMF32528, QMF32534, QMF32535, QMF32541, QMF32542, QMF32549, QMF32572, QMF32575, QMF32600-2, QMF32606, QMF32607, QMF32634.

DESCRIPTION

Fragmentary shoots reaching 13cm long, 1cm wide, bearing spirally arranged scale-like rhomboid (Fig. 7C), elliptical (Fig. 7A), or lanceolate (Figs 7B,D,E; 8E,F) leaves. Leaf dimensions and orientation vary in a sequential (seasonal?) manner along the axis. Larger (lanceolate) leaves typically twisted at base to lie roughly in a common plane (Figs 7A,B,D,E; 8F). Smaller (scale-like) leaves apparently maintained in a spiral arrangement (Fig. 7C) although flattened by sediment compaction. Leaves parallel-veined, 12-16 veins per cm across mid-lamina; apex broadly rounded to pointed acute, rarely acuminate (Fig. 8D); bases contracted, leaving a transversely elliptical, slit-like, or crescentic scar when detached (Fig. 8E). Leaves reaching >10cm long and 25mm wide. Leaf length:width ratio 1.5:1 to 15:1. Beyond basal flexure leaves are straight, gently curved distally, or reflexed; typically arched at 40-90° to axis.

COMPARISON AND REMARKS

Foliage-bearing axes of this species represent the most robust conifer remains from the Winton Formation. The largest specimen from L406 illustrated by Dettmann et al. (1992, fig. 15d) shows three attached branchlets with leaves varying from short spine-like or triangular scale-like forms to more typical linear examples in a repeated manner along the axes. Such lamina variation is evident on axes of the extant Bunya Pine (*Araucaria bidwillii*) and is a consequence of climatic seasonality. Of the extant Australasian araucarians, the Winton specimens are most comparable to *A. bidwillii* in terms of leaf size and seasonal variation but the former typically develop more elongate strap-shaped leaves in each growth cycle. Cone scales associated with the

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FIG. 11. cf. *Austrosequoia wintonensis* Peters & Christophel 1978. A, QMF32520, longitudinal imprints of three associated cones, x 2. B, QMF32543, several associated twigs and cones, x 1. C, QMF32530, slender stem with recurved scale-like leaves, x 2. D, QMF32491, slender stem with spirally arranged arched leaves, x 3. E, QMF32528, pair of slender axes with spirally arranged elongate-rhomboid leaf scars, x 4. F, QMF32571, slender stem with awl-shaped leaves, x 3. G, QMF32550, longitudinal imprint of cone borne on stem with spirally arranged scale-like leaves, x 5. H, QMF32536, oblique imprint of cone with peltate scales, x 5. I, QMF32490, slender branched axes associated with cones, x 2. All specimens from L717.

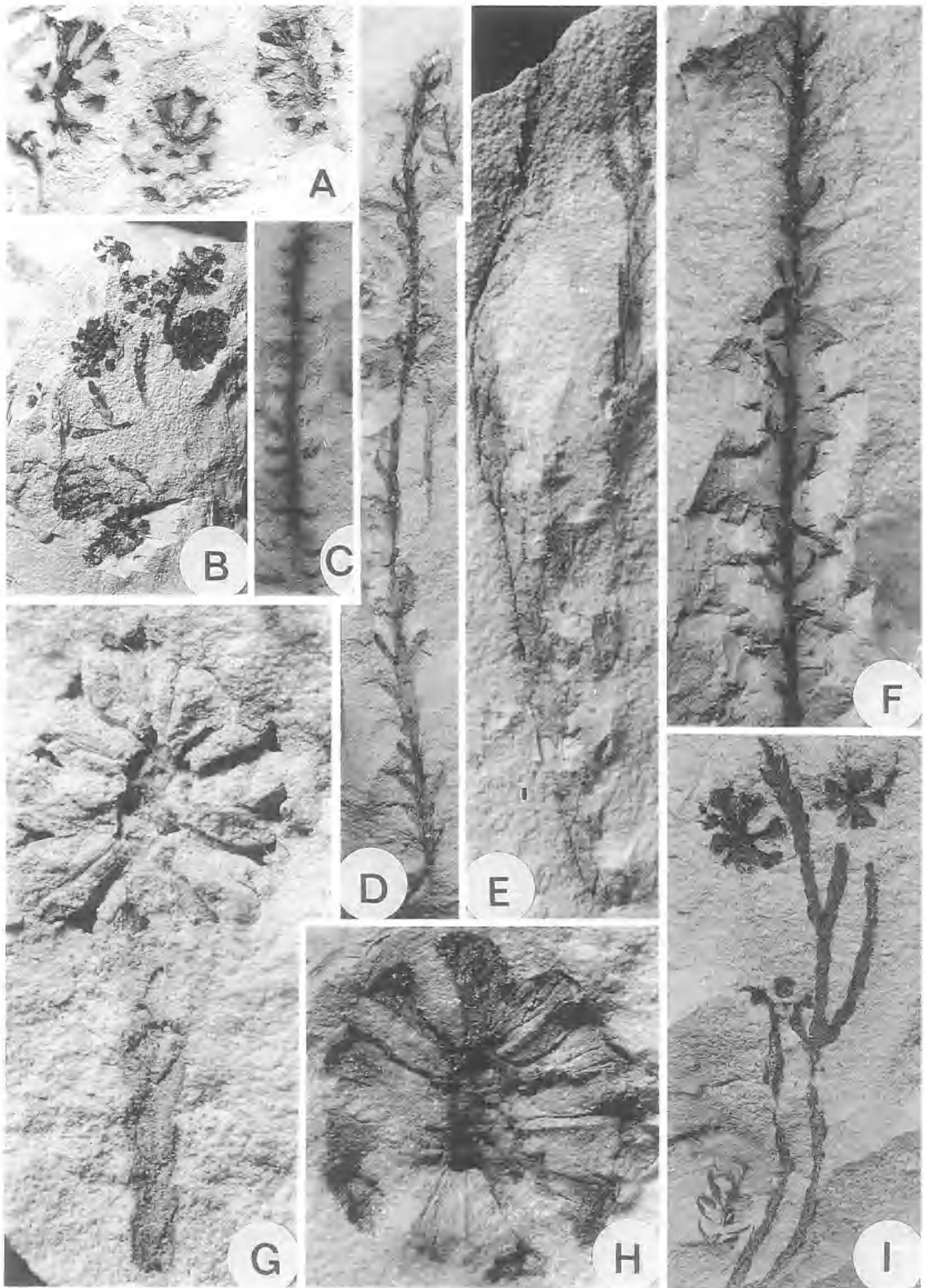


FIG. 11

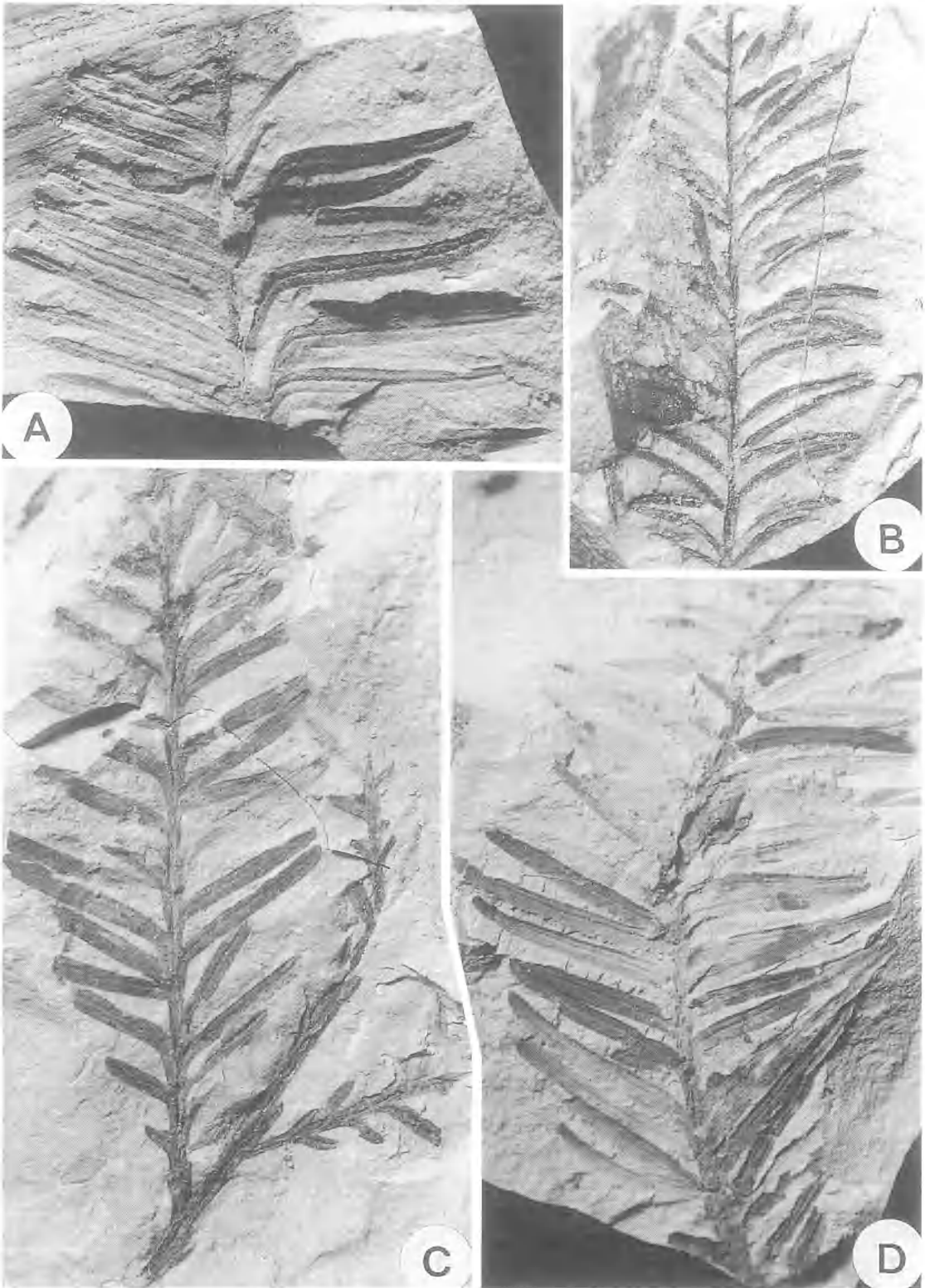


FIG. 12

Winton araucarian foliage are additionally more elongate than *A. bidwillii* scales. *Araucaria cunninghamii* and *A. heterophylla* differ by having consistently smaller scale-like or spine-like leaves. Leaves of the extant New Guinean *Araucaria hunsteinii* differ by their abaxial keel as do leaves of *A. haastii* Ettingshausen emend. Bose from the Late Cretaceous (?Campanian) of New Zealand (Bose, 1975).

Both White's (1974) *Podozamites* sp. and *Equisetites* sp. probably belong to *A.* sp. cf. *A. mesozoica*. Her *Equisetites* sp. appears to represent a detached parallel-veined linear leaflet traversed by several fractures and stain-lines which may have been misinterpreted as nodes.

Walkom's (1919a) *Podozamites kidstoni* Etheridge and *P. lanceolatus* Lindley & Hutton from the Burrum Coal Measures differ from the Winton specimens by their elliptical-oblong leaves with broadly rounded apices. However, his detached leaflets assigned to *Podozamites* sp. have sharply pointed apices similar to the specimens described above. The incompleteness of Walkom's (1919a) *Podozamites* sp. specimen prevents closer comparison although the parallel-veined leaf with a contracted base which he described as *Zamites takuraensis* may belong to the same species. *Araucarites mesozoica* Walkom 1918 has leaves and leaf scars which are very similar to those of the Winton specimens although the few incomplete stems and leaves of this Maryborough Formation species do not show the range of foliar variation evident in examples of the latter. Walkom's (1919b) *Araucarites gracilis* Arber and *Araucarites* sp. from the Jurassic of the Clarence-Moreton Basin, New South Wales, have apically slender and basally tapered two-ranked leaves and may also have close affinities to the Winton specimens. The prominently decurrent bases and narrow laminae of *Podozamites taenioides* Cantrill 1991 serve to distinguish that Victorian Early Cretaceous species from the Winton forms. *Araucaria* sp. cf. *A. heterophylla* (Salisbury) Franco and *Araucaria* sp. of Drinnan & Chambers (1986) from the Victorian Lower Cretaceous differ from the Winton material by their much smaller awl-shaped or imbricate scale-like leaves. The Winton specimens show sufficient variation in their gross foliar morphology to be accommodated within

several araucariacean species (viz., *Araucaria seorsum*, *A. lanceolatus*, *A. acutifolius*, *A. falcatus*, *Agathis victoriensis*) erected by Cantrill (1992) for material from the Victorian Early Cretaceous. Absence of cuticular detail on the Winton specimens prevents critical comparison to Cantrill's (1992) species. *Agathis jurassica* White 1981 from the Middle Jurassic Talbragar Fish Beds differs by its uniform leaves arranged spirally about the stem rather than twisted to form two ranks as shown by the Winton specimens.

New Zealand Late Cretaceous leaves assigned to *Araucarites marshalli* Edwards 1926 are similar to the broader leaves of *Araucaria* sp. cf. *A. mesozoica*. The few and fragmentary specimens of the New Zealand species prevent closer comparison.

Araucarian microsporangiate cones (Fig. 8A-C)

MATERIAL EXAMINED

L406: QMF32446. L717: QMF32492, QMF32499, QMF32532, QMF32538, QMF32598, QMF32603.

DESCRIPTION

Oblong cones reaching 5cm long, 1.7cm wide, consisting of slender (<3mm wide) axis bearing loose, radially disposed distally expanded (peltate?) scales. Scales <7mm long, expanded distally into a 2mm high rhomboid shield. Pollen not preserved.

COMPARISON AND REMARKS

The oblong shape of the cones (Fig. 8A), the diminutive size of the densely spaced, spirally arranged, peltate? bracts (Fig. 8B-C), and their association with ovulate cone scales and araucarian foliage suggests that these organs are araucarian pollen cones. Peterš & Christophel (1978, fig. 17) illustrated a permineralized araucarian cone from the Winton Formation with rhomboid scales similar to the impressions described herein. *Araucarites ?polycarpa* Tenison-Woods of Hill et al. (1966) from the Early Cretaceous of the Stanwell Coal Measures is a slightly larger and better preserved cone showing tightly overlapping bracts. The cone is probably pollen-bearing rather than ovulate as proposed by Hill et al. (1966) and, although larger, may have been a

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FIG. 12. Conifer sp. A. A, QMF32522, slender twig bearing basally arched leaves, x 5. B, QMF32481, slender twig bearing gently arched leaves, x 3. C, QMF32564, branched twigs bearing leaves of variable size, x 3. D, QMF32552, slender twig bearing linear univeined leaves in two ranks. All specimens from L717.

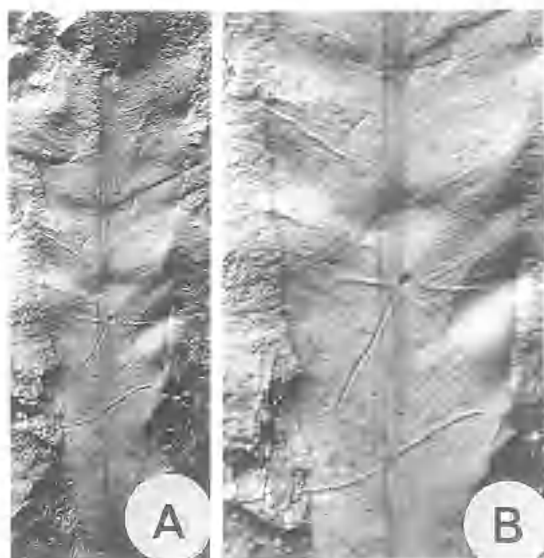


FIG. 13. *Taeniopteris* sp., NMVP199579. A, leaf with prominent midrib and straight secondary veins inserted at 60° to the midvein, x 1. B, details of venation, x 2.

closed immature cone otherwise similar to the Winton specimens. Modern Australian *Araucaria* and *Agathis* species have pollenate cones of similar-shape to the Winton specimens but incomplete preservation and lack of associated pollen with the fossils inhibits closer comparison.

The Winton cones are substantially larger and more oblong than the pollenate cones referred to *Brachyphyllum feistmantelii* and *Nothopheuen brevis* from the Early Cretaceous of Argentina (Baldoni, 1979; del Fueyo, 1991).

Araucarian ovulate cone scales (Fig. 9A-C,E,F,H,I)

Seed cone scales (Araucariaceae). Dettmann et al., 1992: fig. 15e.

MATERIAL EXAMINED

L406: QMF32444, QMF32447. L717: QMF32482, QMF32493, QMF32494, QMF32502, QMF32540, QMF32563.

DESCRIPTION

Triangular-rhomboid cone scales consisting of central triangular strongly vascularized fertile area (Fig. 9A,C,E,I) flanked by marginal poorly vascularized wings. Base tapered but with broad attachment area (Fig. 9C,H); apex varying from broadly rounded to acutely pointed (Fig. 9A-C,E,H); margin entire. Venation divergent di-

chotomous, 10-20 veins per cm adjacent to scale shoulders. Scales 10-37mm long, 7-26mm wide. Shoulders of scales broadly rounded (Fig. 9A) to sharply angled (Fig. 9F). Apical spine <1-5mm long (typically less than one fifth length of scale). Ovule position poorly defined, typically marked by gentle oblong or obovate depression along proximal part of cone scale axis (Fig. 9A,I).

COMPARISON AND REMARKS

All scales are detached although they are sometimes densely clustered on bedding planes. The cone scales display a wide range of sizes and show varying shoulder angles and spine lengths. This variation may be due to their derivation from different plant species, however, the range of shapes and dimensions displayed would not be unexpected within an araucarian species or even within a single cone. The cone scales are commonly associated with foliage of *Araucaria* sp. cf. *A. mesozoica*.

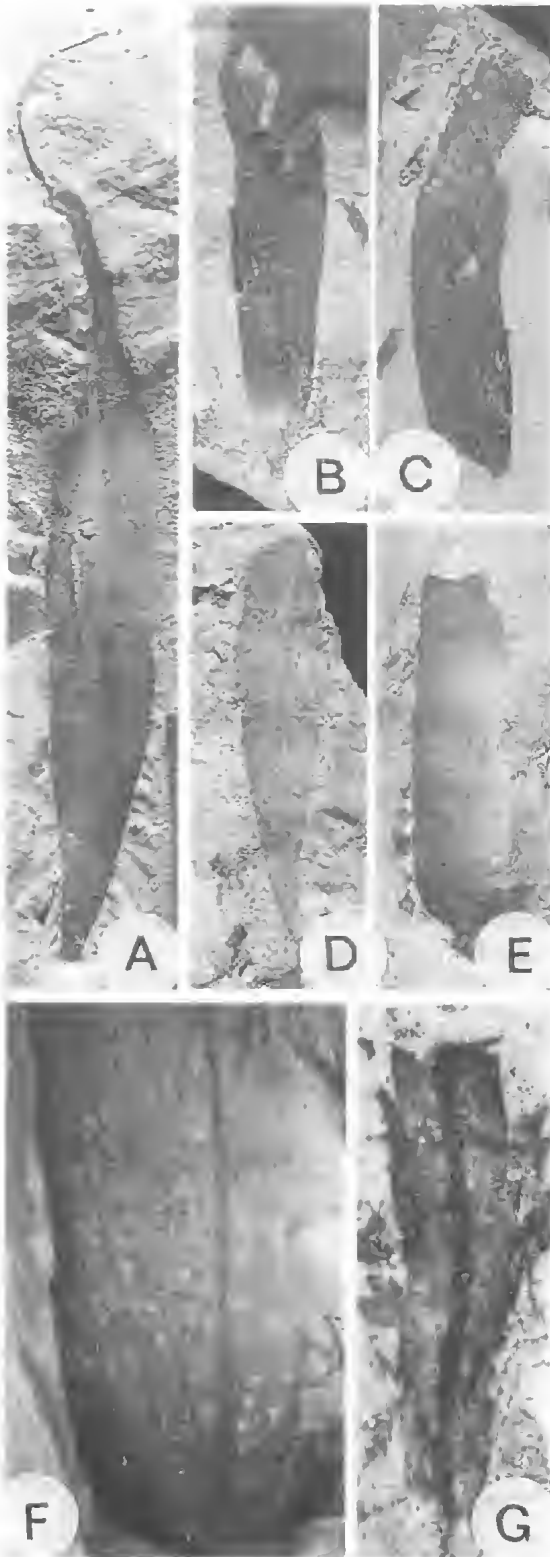
Gondwanan uniovulate conifer cone scales have been assigned to a range of *Araucarites* species based on gross shape, scale dimensions, and prominence of the apical spine. The illustrated differences between many of these species might conceivably be accommodated within an individual cone. We have therefore retained the dispersed Winton cone scales under open nomenclature until attached specimens are found. The most similar Australian cones scales to those presently described are those referred to *Araucarites cutchense* Feistmantel 1876 by Medwell (1954a) and *Araucarites arberi* Walkom 1919a from the Early Cretaceous of Victoria and Queensland (Maryborough Basin) respectively. *Araucarites arberi* has a longer apical spine than the Winton scales but the variation in scale morphology suggests that this may not be a consistent character. Similarly, Medwell's (1954a) specimens fall within the range of morphologies exhibited by the Winton scales.

Family ?PODOCARPACEAE

?*Elatocladus* Halle, 1913
cf. *Elatocladus plana* (Feistmantel)
Seward, 1918
(Figs 9D,G, 10A)

MATERIAL EXAMINED

L717: QMF32515, QMF32613



DESCRIPTION

Slender (<1mm wide) axes with a narrow (<0.5 mm) lateral flange, bearing spirally arranged leaves twisted at their base to lie in a common plane. Leaves univeined, lanceolate to linear, <2mm wide, 10-20mm long. Leaf apex pointed acute; margin entire; base strongly contracted (Fig. 9D,G); petiole negligible. Fructification unknown.

COMPARISON AND REMARKS

This species is distinguished from other conifers in the Winton assemblages by its small, lanceolate to linear univeined leaves, with contracted bases occurring on slender planated branches (Fig. 9d). Similar material from the Gondwanan Jurassic and Cretaceous has frequently been assigned to *Elatocladus confertus* (Oldham & Morris) Halle 1913, *E. heterophylla* Halle, *E. plana* (Feistmantel) Seward, or *Podocarpus* spp. (e.g., Halle, 1913; Arber, 1917; Walkom, 1917; 1919a; 1928; Archangelsky, 1966; Maheshwari & Singh, 1976; Anderson & Anderson, 1985) while Triassic foliage assigned to *Rissikia* species (Townrow, 1967; Anderson & Anderson, 1989) is commonly also similar. In some cases the differences between these taxa are not well-defined and in others (e.g., *E. plana*) foliage of strikingly dissimilar shapes or dimensions has been included in the same species (contrast e.g., Walkom, 1921; White, 1961a; Baksi, 1968). Western Australian Cretaceous forms previously assigned to *E. plana* (Walkom, 1944; White, 1961a) have more needle-like leaves than flattened oblong to linear foliage typical of this species.

Only two specimens comparable to *E. plana* are available in the Winton assemblages. Their lanceolate leaf shape and tapering, pointed apices prevent certain allocation to that species. In these respects the Winton specimens are similar to *Elatocladus longifolium* Baldoni 1980 and *Podocarpus inopinatus* Florin 1940. However, both of these South American Mesozoic species are characterized by very small (<8mm long) leaves attached to long slender axes. The lack of finer morphological detail and fructifications on the Winton specimens prevents comparison with fertile or cuticle-based species such as *E.*

FIG. 14. Angiosperm sp. A. A-E, isolated leaves. A, QMF32579, x 1. B, QMF32451, x 1. C, QMF32448, x 1. D, QMF32452, x 1. E, QMF32449, x 1. F, enlarged detail of fig. 14E showing oblique venation and toothed margin, QMF32449, x 3. G, ?unexpanded leaf, QMF32631, x 10.

Family TAXODIACEAE

cf. *Austrosequoia wintonensis*
Peters & Christophel, 1978
(Figs 10B,D, 11A-I)

Athrotaxis australis Bosc, 1955: 385; pl. 1, fig. 15; pl. 2, figs 16, 17, 24-25; text-fig. 1a.

Athrotaxis selligii Bosc, 1955: 386; pl. 2, figs 18-25; text-figs 1b, 1c.

cf. *Austrosequoia wintonensis* Peters & Christophel, 1978: 3124, figs 2-7.

MATERIAL EXAMINED

L406: QMF32445, L717: QMF32490, QMF32491, QMF32495, QMF32504, QMF32507, QMF32509, QMF32519, QMF32521, QMF32526, QMF32529, QMF32530, QMF32536, QMF32546, QMF32550, QMF32571, QMF32605, QMF32608, QMF32609, QMF32611, QMF32612, QMF32614.

DESCRIPTION

Slender to thick (2-7mm wide) irregularly branched axes bearing helically arranged leaves (Fig. 11D-G). Older (larger) axes typically bearing tightly adpressed, short (<4mm wide, <4mm long) rhomboid scale-like leaves covering entire stem surface or in largest stems separated by <1mm grooves. Small axes bear short (<1mm wide, <2mm long), rhomboid, tightly adpressed, scale-like leaves covering entire stem surface or short (<1mm wide, <3mm long) spinose leaves adpressed to stem, arched away from axis at up to 90° (Fig. 11C), or arched away from axis but distally hooked (Fig. 11D,F). Leaf apices pointed acute becoming obtuse in older leaves. Leaves show broad basal attachment. Slender (ultimate) twigs sometimes attached to cones (Fig. 11B,G,I) reaching 8mm wide, 10mm long, comprising spirally arranged wedge-shaped or peltate scales reaching 4mm long, 2mm deep (Fig. 11A,G,H). Cones commonly open. Distal end of cone scales expanded, rhomboid in lateral view with a central, <0.5mm, depression (on petrifications) or raised tubercle (on impressions). A single spinose 8mm wide, 7mm long ovate organ (QMF32509) attached to a slender scale-bearing terminal twig may represent an under-developed ovulate cone of this species.

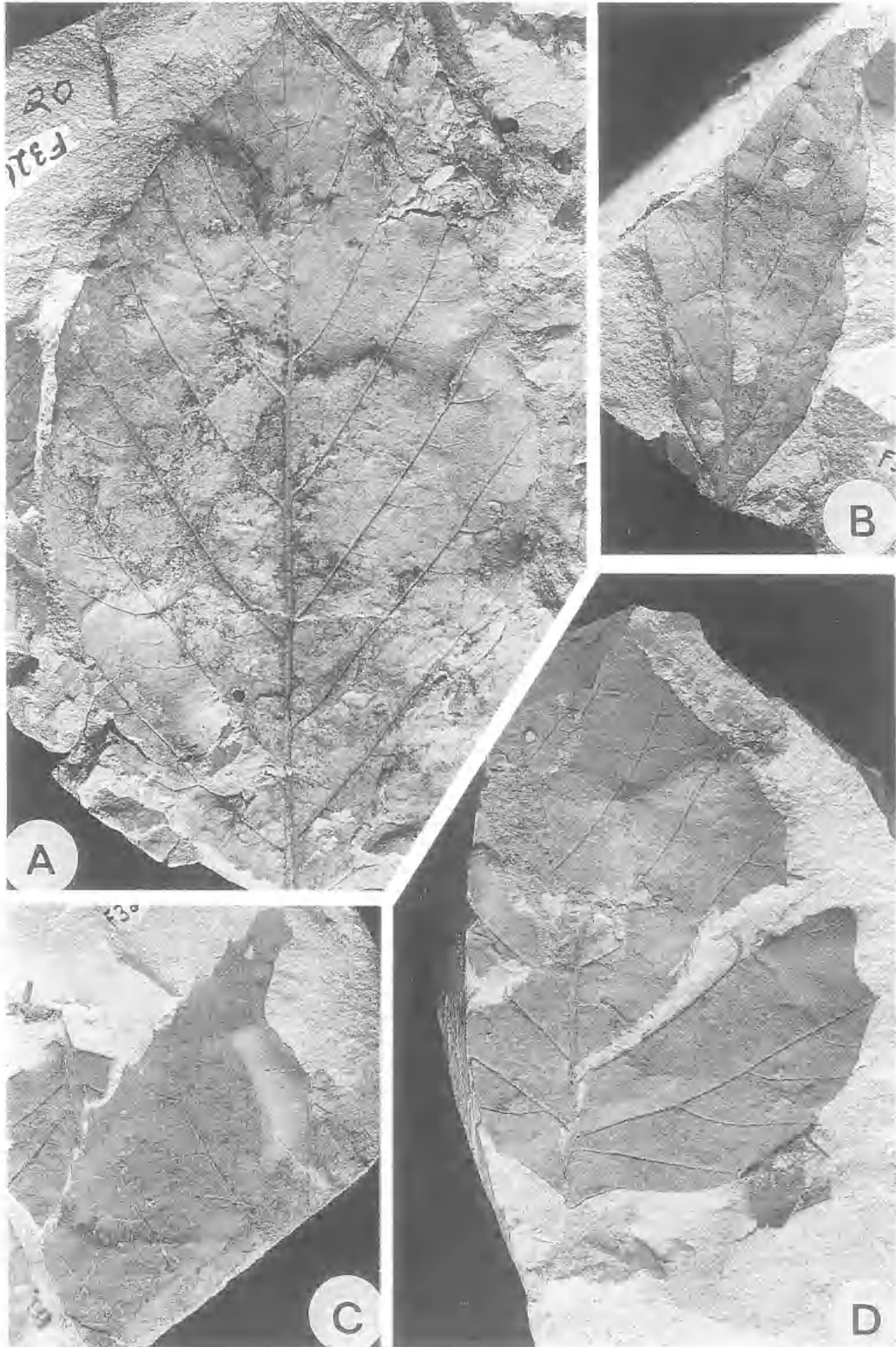


FIG. 15. Angiosperm sp. A, QMF32449, line drawing of specimen in Figs 14E,F showing details of venation. Scale bar: 5mm.

papillosa Baldoni 1980 and *Morenoa fertilis* Del Fueyo, Archangelsky & Taylor 1990. Dimorphic foliage is not evident on the Winton specimens comparable to that claimed for *Elatocladus longifolia* Borkar & Chiplonkar 1973 from the mid-Cretaceous of India.

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FIG. 16. Angiosperm sp. B, isolated leaves. A, QMF32459, x 1. B, QMF32453, x 1. C, QMF32458, x 1. D, QMF32455, x 1.



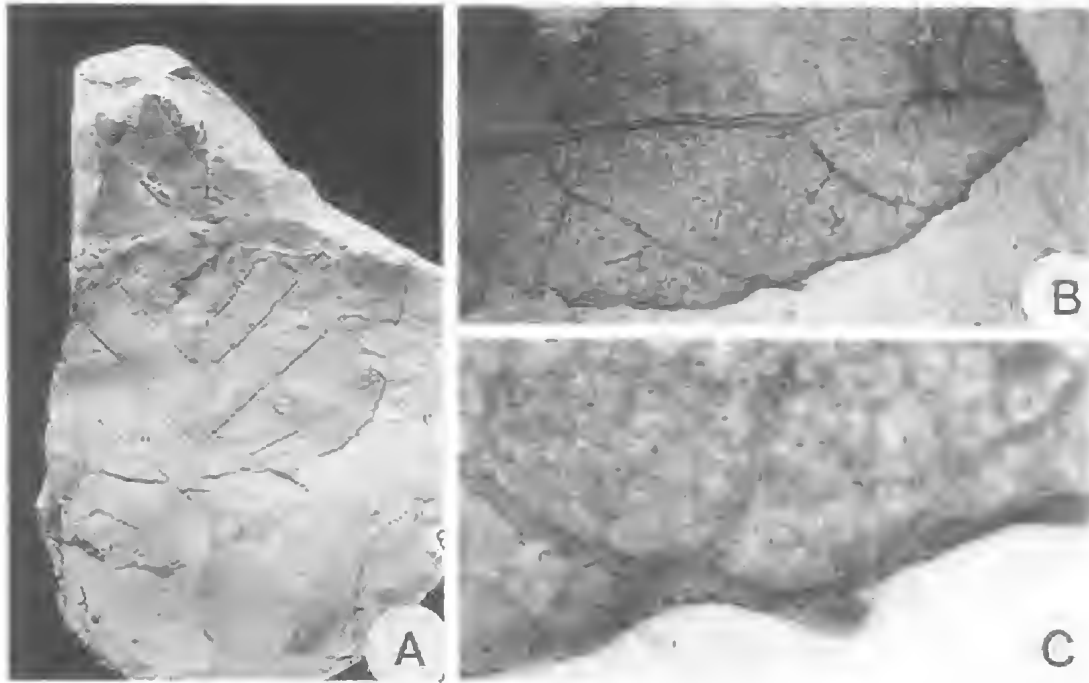


FIG. 17. Angiosperm sp. B, QMF32457. A, isolated leaf, x 0.8. B, detail of leaf margin enlarged from Fig. 17A, x 4. C, detail of leaf-margin tooth enlarged from Fig. 17B, x 15.

COMPARISON AND REMARKS

The axis impressions, sometimes with attached cones, are morphologically identical to surface features evident on permineralized cones and foliage bearing axes assigned to *Austrosequoia wintonensis* by Peters & Christophel (1978). However, their conspecific nature can not be confirmed as *A. wintonensis* was defined largely upon anatomical features not available in the impressions. Cone impressions and casts assigned to *Athrotaxis sellingii* by Bose (1955) appear to be identical to the Winton material. His foliage-bearing axes (*Athrotaxis australis* Bose) are also closely comparable to the Winton specimens although some leaves of *A. australis* appear to have more attenuated apices. We consider that *Athrotaxis australis*, *Athrotaxis sellingii*, *Austrosequoia wintonensis*, and the impressions described here are probably conspecific but have previously been described as separate species owing to their differing fossilization states and incomplete preservation. Of these taxa *Athrotaxis australis* has nomenclatural priority, however, the anatomical studies of Peters & Christophel (1978) show that the ovulate cones have an architecture differing in several respects from extant *Athrotaxis* species. We propose the retention of *Austrosequoia wintonensis* for anatomically preserved remains but

place those specimens lacking cellular details under more open nomenclature.

Foliage and ovulate cones of *Sequoia novaezeelandiae* Ettingshausen 1891 from the Upper Cretaceous of New Zealand are possibly also conspecific with the Winton specimens. The New Zealand example possesses a short spine on the tip of the cone scales. This feature has not been detected on the Winton cone impressions although some of the permineralized cone scales of *Austrosequoia wintonensis* illustrated by Peters & Christophel (1978) show a low protuberance.

Broad, scale-like leaves on larger branches amongst the present material are comparable in shape to the rhomboidal, spirally inserted, imbricate leaves of the extant Tasmanian *Athrotaxis cupressoides* and the Early Tertiary Tasmanian *Athrotaxis ungeri* (Halle) Florin 1940. Slender terminal axes from the Winton Formation commonly also show short spinose leaves similar to *Athrotaxis selaginoides*. *Athrotaxis tasmanica* Hill, Jordan & Carpenter from Oligocene sediments of Tasmania is distinguished by the prominent abaxial keels on its leaves (Hill et al., 1993). The spinose leaves within the range of foliage attributed to cf. *Austrosequoia wintonensis* also fall close to the dimensions of some leaves referred herein to "Conifer indet." although the

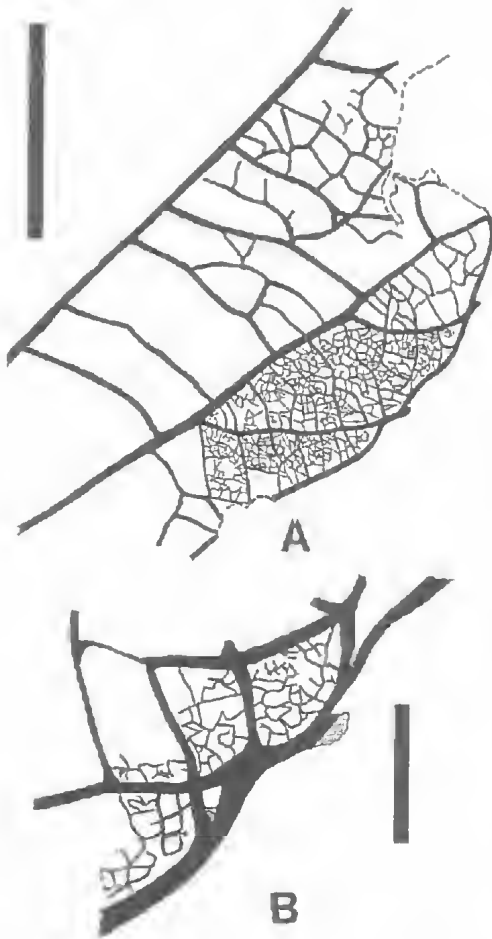


FIG. 18. Angiosperm sp. B, QMF32457. A, line drawing showing venation detail from Fig. 17B. B, line drawing showing venation detail from Fig. 17C. Scale bars: A = 10mm, B = 2mm.

latter are typically flattened and are not distally hooked.

Family UNCERTAIN

Conifer sp. A (Figs 10C, 12A-D)

MATERIAL EXAMINED

L406: QMF32615, NMVP199579. L717: QMF32481, QMF32497, QMF32522, QMF32531,

QMF32547, QMF32552, QMF32564, QMF32604, QMF32610, QMF32616, QMF32617.

DESCRIPTION

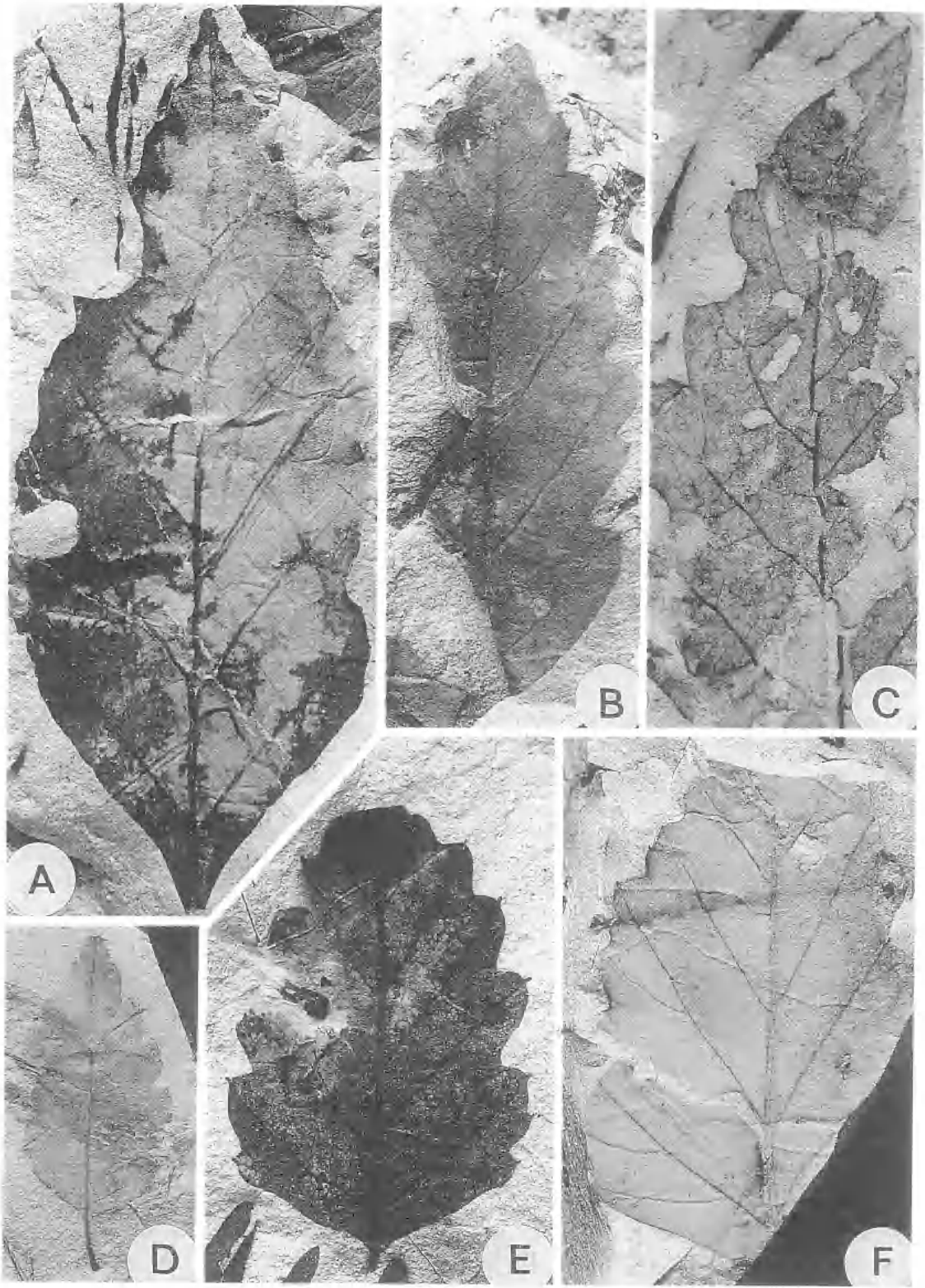
Slender (<2mm wide) axes bearing variable spirally inserted leaves. Shoots <4.2cm long, mostly detached, rarely branched irregularly. Leaves range from diminutive (<0.5mm wide, <1.5mm long) scale-like appendages adpressed against the axis (Figs 10C, 12C) to linear (<1mm wide, 12mm long) needles strongly arched away from the axis (Fig. 12A-D). Leaf base slightly clasping?, twisted to align leaves in a common plane (Fig. 12C). Longer leaves commonly arched sharply <2mm above base then gently flexed distally, remaining straight, or gently reflexed (up to 70° to axis) along outer part of lamina (Fig. 12A). Fructifications unknown.

COMPARISON AND REMARKS

This conifer species shows a broad range of foliage types some of which are morphologically similar to certain examples of cf. *Elatocladus plana* and cf. *Austrosequoia wintonensis* occurring at the same locality. However, Conifer sp. A is distinguished by its slender (needle-like) leaves which are strongly arched (but not contracted) near the base to align the leaves in two ranks. Several extant conifer genera produce superficially similar foliage. The lack of cuticular details and fructifications inhibits confident attribution of these remains to any genus. A possible affinity with the Taxales is suggested by their slender, slightly flattened, needle-like, univeined, seasonally variable, two-ranked leaves which appear to have been consistently shed while still attached to the terminal twigs.

Conifer sp. A is most similar to *Podocarpus hochstetteri* Ettingshausen 1891 from the New Zealand Upper Cretaceous which has similar straight or falcate leaves which are strongly arched at the base. Better material from the *P. hochstetteri* type locality is required for more detailed comparison. The Winton specimens are also closely comparable to several foliage-bearing twigs variously assigned to *Elatocladus confertus* or *Elatocladus plana* from the Australian Jurassic and Cretaceous (Walkom, 1919a, 1928; Hill et al., 1966).

FIG. 19. Angiosperm sp. C, isolated leaves. A, QMF32489, x 1.6. B, QMF32557, x 1.75. C, QMF32554, x 1.8. D, QMF32559, x 1.5. E, QMF32562, x 1.5. F, QMF32517, x 1.5.



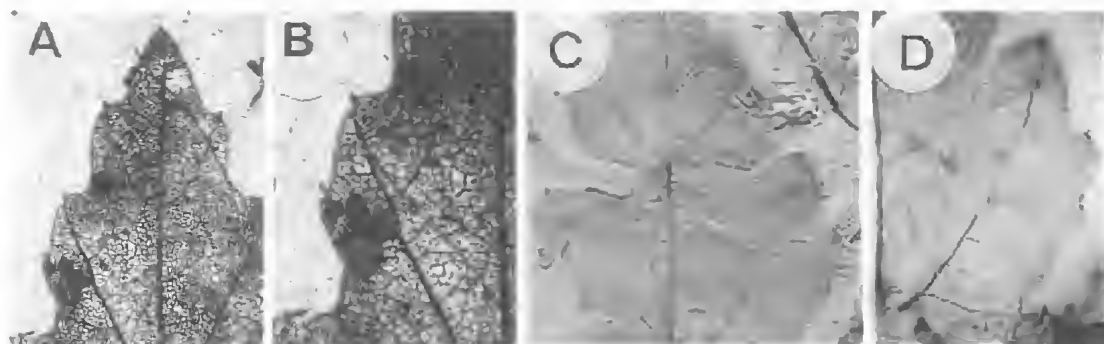


FIG. 20. Angiosperm sp. C. A, QMF32524, isolated leaf, x 2. B, QMF32524, detail of leaf margin enlarged from Fig. 20A, x 3.2. C, QMF32512, isolated leaf, x 1.5. D, QMF32512, detail of leaf margin enlarged from Fig. 20C, x 2.

Incertae sedis
Order PENTOXYLALES
Family PENTOXYLACEAE

Taeniopteris Brongniart, 1828
Taeniopteris sp.
(Fig. 13)

MATERIAL EXAMINED

L406: NMVP199580, NMVP199581.

DESCRIPTION

?Spathulate entire or slightly undulate-margined leaves, apex and base absent from both specimens. Leaves reaching in excess of 70mm long and 22mm wide. Arrangement on axis uncertain. Stout midrib reaching 2mm wide near base, tapering slightly towards apex. Lateral veins depart midrib at 60°-70° and pass straight to the margin without branching or with one, rarely two, dichotomies. No marginal vein present. Vein concentration 23-28 per cm along margin. Fructifications and cuticular details unavailable.

COMPARISON AND REMARKS

Although these leaves are not associated with fructifications they are morphologically similar to taeniopterid leaves from Early and mid-Cretaceous strata elsewhere in Australia and are here regarded as most probably pentoxylalean. Similar leaves are produced by some ferns (e.g., *Asplenium*) hence a pteridophytic affinity can not be entirely excluded.

The few specimens and incomplete preservation of the available material prevents detailed comparison with other species. However, *Taeniopteris* sp. differs from the widespread Australasian Early Cretaceous *T. daintreei* McCoy

1874 and the morphologically similar Indian *T. spatulata* Oldham & Morris 1863 by the lesser angle of departure of the secondary veins from the midrib. *Taeniopteris elongata* Walkom 1918 from the Maryborough Formation (Aptian) also has secondary veins oriented at around 90° to the midrib and may be synonymous with *T. daintreei*. *Taeniopteris howardensis* Walkom 1919 from the Burrum Coal Measures (Albian), Maryborough Basin, is morphologically closest to *Taeniopteris* sp. in having secondary veins at around 70° to the midrib although the venation density in the former is reportedly much greater. *Taeniopteris stipulata* Hector 1886 from the Late Cretaceous of New Zealand (McQueen, 1956) is also closely comparable in its venation orientation although it appears to be represented by narrow elliptical or lanceolate leaves.

Division MAGNOLIOPHYTA
Class MAGNOLIOPSIDA
Subclass UNCERTAIN

Angiosperm sp. A
(Figs 14A-G, 15)

MATERIAL EXAMINED

L406: QMF32448, QMF32449, QMF32451, QMF32452, QMF32579. L552: QMF32631.

DESCRIPTION

Leaves; lamina up to 125mm long and 12mm wide, linear, with a cuneate base and a long, attenuate apex, petioles not preserved. Margin serrate, each tooth terminating a secondary vein. Primary venation pinnate, secondary venation simple craspedodromous; midvein straight or slightly curved; secondary veins closely spaced,

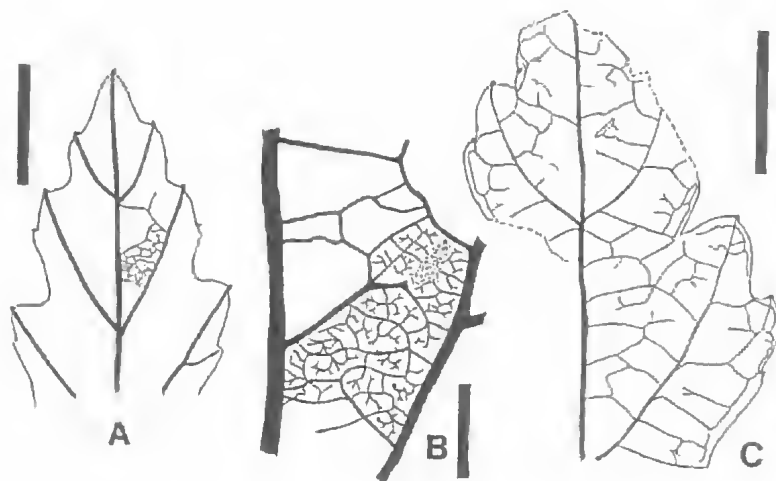


FIG. 21. Angiosperm sp. C. A, QMF32524, line drawing of specimen in Fig. 20A. B, QMF32524, detail of venation enlarged from Fig. 21A. C, QMF32512, line drawing showing detail of venation of specimen in Fig. 20C. Scale bars: A, C = 10 mm, B = 2 mm.

arising from midvein at 30° angle; tertiary veins linking secondary veins, but indistinct.

COMPARISON AND REMARKS

A single specimen has the complete lamina preserved and shows the base and apex shape (Fig. 14A). It has a lamina 100mm long, which extends another 25mm as a long, narrow, attenuate apex. The other five specimens are fragmentary, but exhibit the acute secondary veins terminating in widely-spaced, distally pointing, serrations along the otherwise entire leaf margin (Fig. 14B-G). A reticulate network of tertiary veins toward the margin is just evident in one specimen (Figs. 14F, 15), but otherwise higher order venation is unclear. One very small, possibly not fully expanded, leaf from L552 shows the leaf margin's teeth well developed but no secondary or higher order venation (Fig. 14G).

Subclass HAMAMELIDAE
Order ?FAGALES
Family UNCERTAIN

Angiosperm sp. B
(Figs 16A-D, 17A-C, 18A,B)

MATERIAL EXAMINED

L406: QMF32453-60, QMF32577. L717: QMF32556, QMF32583. L552: QMF32468-71. Conway's Claim: ?QMF17458.

DESCRIPTION

Leaves; lamina up to 145mm long and 70mm wide, ovate to elliptical, with asymmetrical cuneate base and acuminate tip; petioles reaching 36mm long. Margins entire to gently lobed or slightly serrate about secondary vein endings, which are terminated by a short setaceous tooth. Primary venation pinnate, secondary venation simple craspedodromus; midvein straight; secondary veins 14 to 16, paired basally, diverging at 50° , upper veins sometimes more acute than lower veins; prominent tertiary veins oriented obliquely with respect to midvein, linking secondary veins; quaternary and higher order veins forming irregular polygonal areoles

with branched veinlets. Secondary veins with exmedial branches that become continuous distally to form a distinct fimbrial vein along the leaf margin.

COMPARISON AND REMARKS

The twelve specimens listed above show minor variation in leaf shape and venation. Several specimens are elliptical with entire margins and uniformly diverging secondary veins (Fig. 16A,B). Several other leaves are relatively broader, tend to be ovate, have slightly lobed margins, and have their more proximal secondary veins diverging from the midvein at a less acute angle than those distally (Figs 16D, 17A). The narrower specimens tend to have a more cuneate base, but in all specimens where the base of the lamina is preserved it is distinctly asymmetrical. All specimens have identical higher order venation, and have the exmedial secondary vein branches continuous as a marginal fimbrial vein that supplies a short, setaceous tooth at the point where each secondary vein or one of its branches reaches the leaf margin (Figs 17A-C, 18A,B).

These leaves are similar in size and venation to several taxa Pole (1992) described from Cenomanian localities of the Matakaea Group, New Zealand (parataxa MATA-1 Pole 1992: figs 2, 3, and MATA-2 Pole 1992: fig. 4). All are relatively large hamamelid leaves with simple

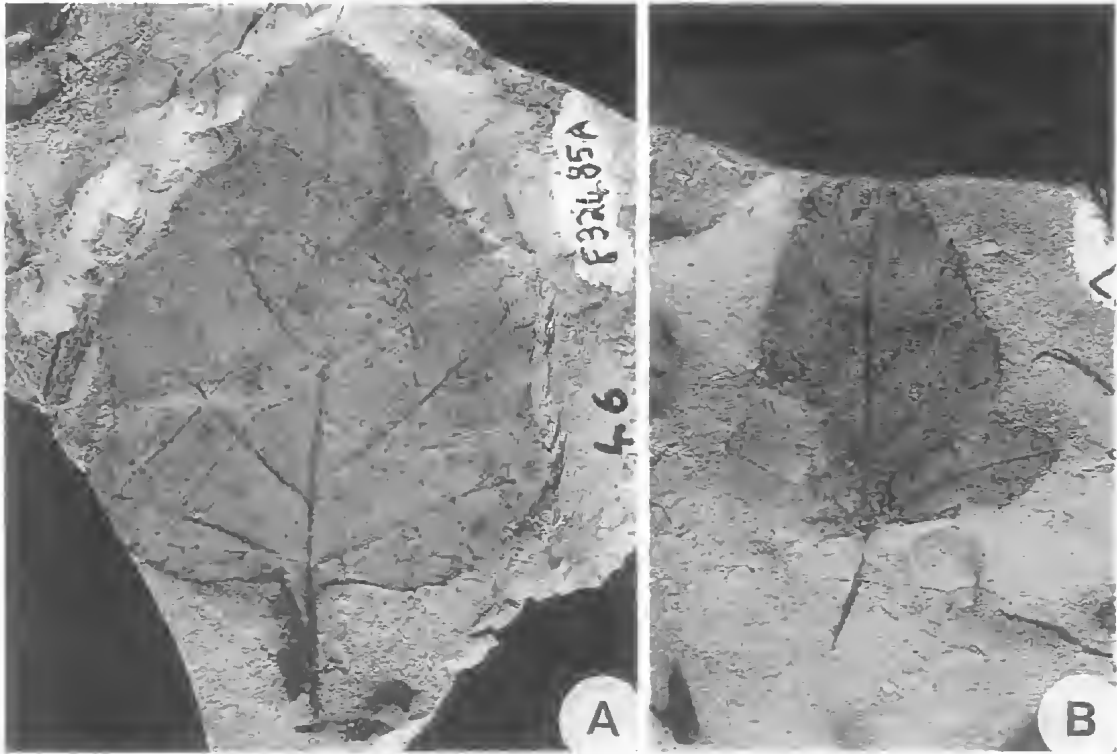


FIG. 22. Angiosperm sp. D, isolated leaves. A, QMF32485, $\times 1.4$; B, QMF32487, $\times 1.5$.

craspedodromous venation and prominent, obliquely oriented, tertiary veins.

Angiosperm sp. C
(Figs 19A-F, 20A-D, 21A-C)

MATERIAL EXAMINED

L717a: QMF32483, QMF32486, QMF32489, QMF32506, QMF32508, QMF32510-12, QMF32517, QMF32523, QMF32524, QMF32539, QMF32554, QMF32557, QMF32559, QMF32562, QMF32565, QMF32566, QMF32568-70, QMF32573, QMF32581, QMF32582, QMF32584-91.

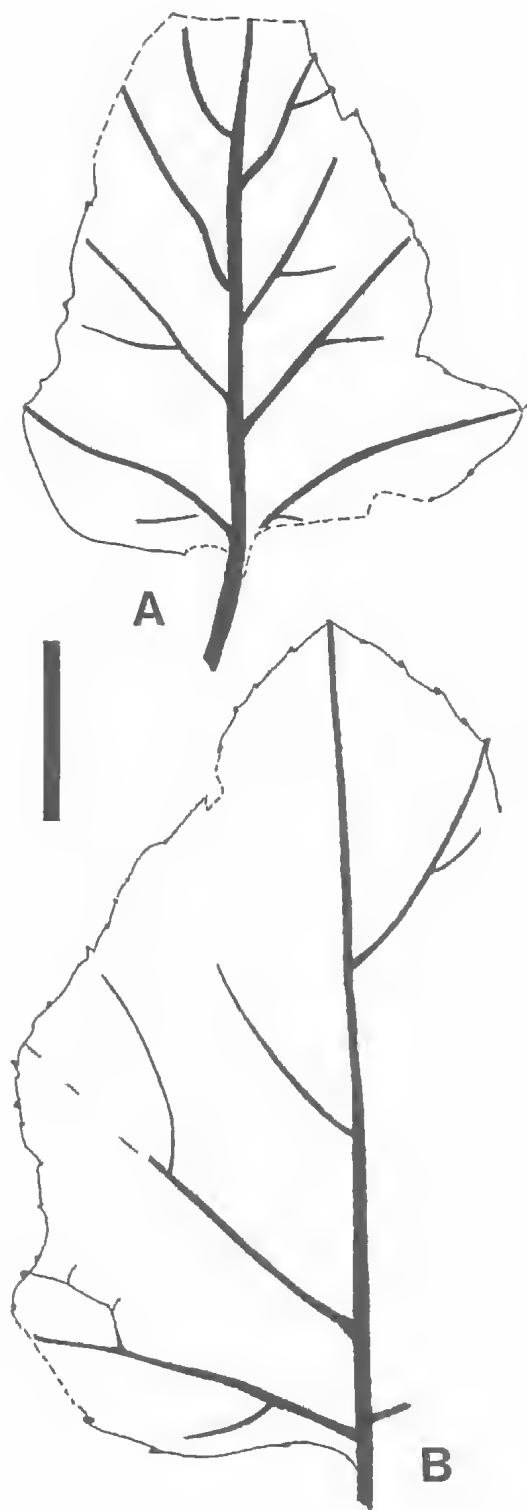
DESCRIPTION

Leaves; lamina up to 95mm long and 46mm wide, ovate to elliptical, with obtuse to cuneate base and acute to slightly mucronate apex, petioles preserved up to 6mm long. Margins lobed about secondary veins, which terminate in a mucronate tooth; smaller leaves are mucronate only at secondary vein endings, larger leaves have exmedial secondary vein branches terminating serrulations. Primary venation pinnate, secondary venation simple craspedodromous; midvein straight; secondary veins 10-14, paired basally,

diverging from midvein at $35-60^\circ$, upper veins more acute than lower veins; tertiary veins randomly oriented; higher order veins forming a random reticulate network of areoles with twice branched veinlets.

COMPARISON AND REMARKS

This is the most numerous Winton angiosperm leaf type, with approximately 20 specimens examined from L717. They are superficially similar to Angiosperm sp. B from L406 in their general shape and simple craspedodromous venation, but they are generally much smaller and differ in several other respects. Their margins are more deeply lobed, and the secondary veins and their branches do not form a prominent fimbrial vein (Figs 20A-D, 21C). Tertiary veins are not as prominent as those of Angiosperm sp. B, and they are randomly oriented rather than consistently oblique to the midvein. Higher order veins form a network of areoles with branched veinlets (Fig. 21A,B). Leaf margins are relatively deeply lobed, each lobe with a mucronate tooth at its apex, which terminates a secondary vein; in larger leaves, exmedial secondary vein branches may also supply a toothed lobe, especially in the prox-



imal portion of the leaf. The sinus between each lobe is gently rounded. The midvein extends to the apex of the leaf, and also terminates in a mucronate tooth. Morphological variation is similar to that seen in Angiosperm sp. B and extant hamamelids; some leaves are elliptical (Fig. 19A,B), others ovate (Fig. 19E,F). The more ovate leaves tend to have a decreasing secondary vein divergence angle from base to apex, and more strongly developed secondary vein branched proximally (Fig. 19E,F). In some leaves, only the basal pair of secondary veins are opposite, in others up to four pairs are oppositely arranged in the proximal half of the leaf. Only one small leaf has the petiole preserved intact; it is 6mm long and the lamina is 29mm long (Fig. 19D).

These leaves are reminiscent of *Nothofagus praequercifolia* (Ett.) Pole recorded from Santonian to early Maastrichtian localities in the Taratu Formation, New Zealand (Pole, 1992). Features in common are the lobed leaf margin with mucronate tips, and simple craspedodromous venation with irregularly oriented tertiary veins (see Pole, 1992: figs. 23-31). Several incomplete Winton specimens may have had more deeply dissected margins, resembling *Nothofagus melanoides* Pole, also from the Taratu Formation.

Angiosperm sp. D
(Figs 22A,B, 23A,B)

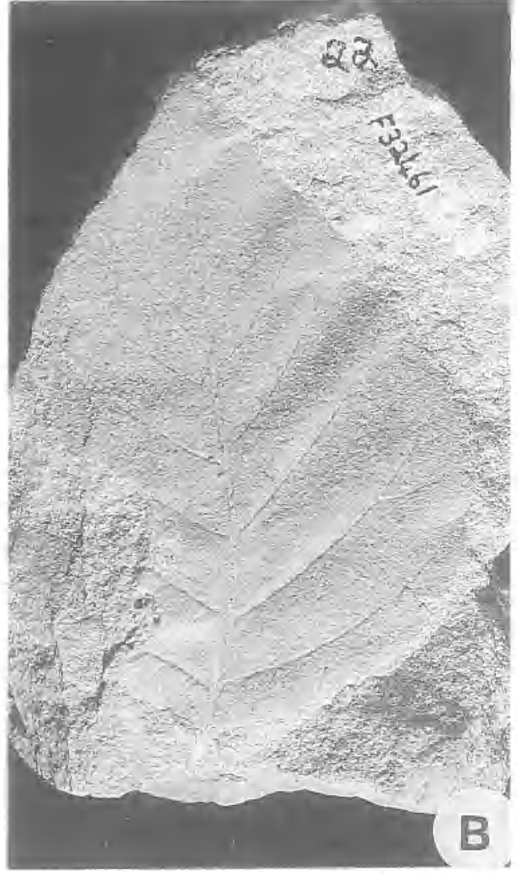
MATERIAL EXAMINED

L717: QMF32485, QMF32487.

DESCRIPTION

Leaves; lamina up to 52mm long and 45mm wide, ovate, with an obtuse base and obtuse apex with mucronate tip, petiole 10-12mm long. Margins slightly lobed about secondary veins, and serrulate with mucronate teeth terminating secondary veins and their exmedial and occasional admedial branches. Primary venation pinnate, secondary venation simple craspedodromous; midvein straight; secondary veins 10, paired basally, diverging from midvein at 45-50°, upper veins more acute than lower veins; higher order venation not preserved.

FIG. 23. Angiosperm sp. D, line drawings of isolated leaves. A, QMF32487. B, QMF32485. Scale bar: 10mm.



COMPARISON AND REMARKS

Only two specimens of this leaf type were identified. They are distinguishable from *Angiosperm* sp. C, from the same locality, by their gently lobed rather than dissected outline and their almost deltoid shape. One specimen has such strongly developed basal segments it is almost trilobed (Figs 22B, 23A). The margin is serrate, each serration having a dark, glandular appearance. Some of these serrations clearly terminate a secondary vein or exmedial secondary vein branch, and the others probably also terminate a secondary vein or its branches. There is no evidence of a marginal, fimbrial vein.

Angiosperm sp. E
(Fig. 24A,B)

MATERIAL EXAMINED

L224: QMF32461-3.
L165: QMF32464, QMF32593.

DESCRIPTION

Leaves; lamina up to 80mm long and 60mm wide, ovate, with asymmetrical base, apex not preserved. Primary venation pinnate, secondary venation simple craspedodromus; midvein curved; secondary veins 12-16, diverging from midvein at 45-60°, paired proximally; tertiary venation prominent, oblique to midvein; higher order venation not preserved. Margins more or less entire.

COMPARISON AND REMARKS

Three specimens of this leaf type are preserved from L224. They are poorly preserved in a coarse, white, sandy matrix, and do not show the same fine detail as specimens from other Winton locations, making comparison difficult. They most closely resemble the more ovate specimens of *Angiosperm* sp. B from L406 having similar size, asymmetrical base, and prominent, oblique, tertiary venation, and may be conspecific with those leaves. The main differences are that two specimens have a curved midvein (although this may be taphonomic deformation, Fig. 24A,B), and two of the three leaves have some secondary veins that dichotomize rather than produce exmedial branches. The coarse nature of the sedi-

ment precludes assessment of the presence or absence of a fimbrial vein.

Angiosperm sp. F
(Fig. 24C)

MATERIAL EXAMINED

L406: QMF32450.

DESCRIPTION

Leaf; lamina greater than 65mm long, 50mm wide, prominent midvein, margin deeply cleft.

COMPARISON AND REMARKS

Only one specimen is known from L406. It is poorly preserved, the venation pattern is not evident, and the specimen shows no details other than gross outline of the margin. It looks superficially like the most dissected leaves of *Angiosperm* sp. C from L717, but little else can be said of its affinities.

Angiosperm sp. G
(Fig. 24D)

MATERIAL EXAMINED

?L717 Dalkeith: QMF18106.

DESCRIPTION

Leaf; lamina greater than 75mm long, 45mm wide, ovate, attenuate apex, base not preserved. Margins cleft about secondary veins and their exmedial branches, each tooth terminated by a mucronate tip. Primary venation pinnate, secondary venation simple craspedodromus; midvein straight or slightly curved; secondary veins c. 10, paired in proximal portion of leaf, diverging from midvein at 20-30°, higher order venation not preserved.

COMPARISON AND REMARKS

This leaf type is represented by a single specimen (Fig. 24D). It is distinguished from other Winton angiosperms by its attenuate apex, serrate margin that is more or less equally cleft between the secondary veins and exmedial secondary vein branches, and acutely angled sinuses between serrations. Pole (1992: fig 40) illustrated a similar leaf (parataxon TARA-18) from the early

previous page

FIG. 24. A, B, *Angiosperm* sp. E, isolated leaves. A, QMF32462, x 1, B, QMF32461, x 1. C, *Angiosperm* sp. F, QMF32450, leaf fragment, x 1, D, *Angiosperm* sp. G, QMF18106, isolated leaf, x 1. E-H, *Angiosperm* sp. H, isolated leaves, E, QMF32474, x 1.9. F, QMF32472, x 1.8. G, QMF32473, x 2. H, QMF32475, x 2.

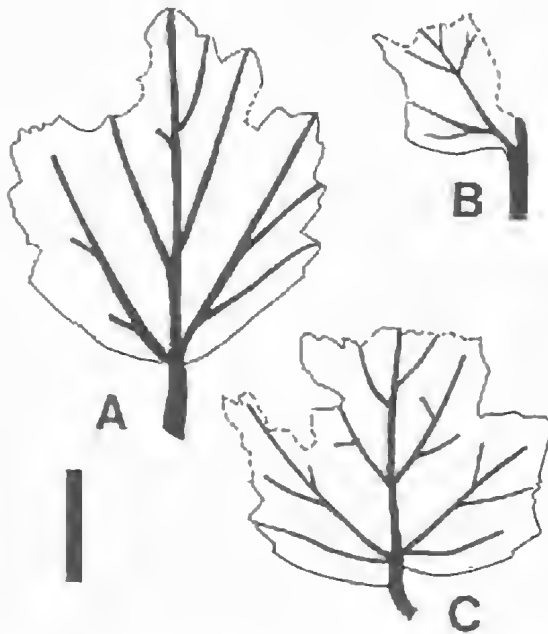


FIG. 25. *Angiosperm* sp. H, line drawings of isolated leaves. A, QMF32474. B, QMF32632. C, QMF32472. Scale bar: 5mm.

Maastrichtian of the Taratu Formation, New Zealand, which he tentatively assigned to *Betulaceae*.

***Angiosperm* sp. H**
(Figs 24E-H, 25A-C)

MATERIAL EXAMINED

L552: QMF32472-5, QMF32592, QMF32632.

DESCRIPTION

Leaves; lamina up to 20mm long and 20mm wide, ovate, with cordate to obtuse base and obtuse apex, petiole preserved up to 3mm. Venation simple craspedodromous; midvein straight; secondary veins c.8, diverging from midvein at 45-60°, paired basally; higher order venation not preserved. Margins incised, more deeply cleft about main secondary veins than secondary vein branches.

COMPARISON AND REMARKS

These are the smallest of the Winton angiosperm leaves. Only a few specimens are complete, but there are numerous lamina fragments in matrix from L552. The largest complete leaf has a lamina 20mm long, but a few of the dispersed lamina fragments suggest some leaves were slightly larger. There is some possibility that they are unexpanded leaves of

one of the previously described taxa, possibly *Angiosperm* sp. B, which also occurs at the same locality. The veins and lamina have the appearance of being relatively thick, and some fragments look to belong to leaves attached to the same shoot. There are numerous twigs associated with the leaves, and the dense accumulation of leaves and lamina fragments in the matrix may derive from a single branch.

**WINTON ASSEMBLAGES IN RELATION
TO OTHER CRETACEOUS FLORAS**

The Winton Formation assemblages differ slightly in their taxonomic composition (Table 1) and their stratigraphic relationships to one another are uncertain. However, the presence of some shared taxa between localities suggests that the assemblages are more or less coeval. The fossils, varying from delicate fern fronds to robust conifer branches, and including a series of ginkgophyte, pentoxylalean, and angiosperm leaf types, suggest that the assemblages were derived from diverse plant communities of herbaceous and woody plants. The relatively complete preservation of several leaf types suggests an absence of turbulent transport to their site of deposition and implies that most if not all the remains were derived from very local sources. The Winton Formation suites, therefore, show the earliest Australian microfossil representation of a vegetation type comprising abundant and diverse angiosperms mixed with typical Mesozoic fern and gymnosperm elements (Fig. 26).

The earliest unequivocal evidence of flowering plants are monosulcate pollen grains from the Hauterivian (middle Early Cretaceous) of Israel (Brenner, 1984) and southern England (Hughes & McDougall, 1987). Monosulcate or monosulcate-derived pollen is characteristic of extant magnoliid dicotyledons and monocotyledons. Triaperturate pollen diagnostic of the non-magnoliid ("higher") dicotyledons appears slightly later at around the Barremian-Aptian boundary. A subsequent major diversification of angiosperms through the mid-Cretaceous is clearly established from analyses of both megafloras and palynofloras (Hickey & Doyle, 1977; Lidgard & Crane, 1988, 1990; Crane & Lidgard, 1989, 1990). In the Northern Hemisphere angiosperm pollen first appears and becomes both abundant and diverse at low palaeolatitudes, and only subsequently becomes important in middle and high palaeolatitudes (Hickey & Doyle, 1977; Crane & Lidgard, 1989). There are less data for the South-

TABLE 1. Distribution of fossil plant taxa at Eromanga Basin localities.

Species	L406	L717	L552	L224	L165	Conway's Claim
<i>Phyllopteroides macclymontae</i>		+				
<i>Microphylopteris</i> sp. cf. <i>M. gleichenoides</i>			+			
<i>Cladophlebis</i> sp.		+	+			
<i>Sphenopteris</i> sp. cf. <i>S. warragulensis</i>			+			
<i>Sphenopteris</i> sp.		+				
indeterminate fern pinnule		+				
<i>Taeniopteris</i> sp.	+					
<i>Ginkgo wintonensis</i>		+				
<i>Araucaria</i> sp. cf. <i>A. mesozoica</i>	+	+				
Araucarian microsporangiate cones	+	+				
Araucarian ovulate cone scales	+	+				
<i>Elatocladus</i> sp. cf. <i>E. plana</i>		+				
cf. <i>Austrosequoia wintonensis</i>	+	+	?			
Conifer sp. A	+	+				
Angiosperm sp. A	+		+			
Angiosperm sp. B	+	+	+			?
Angiosperm sp. C		+				
Angiosperm sp. D		+				
Angiosperm sp. E				+	+	
Angiosperm sp. F	+					
Angiosperm sp. G		+				
Angiosperm sp. H			+			

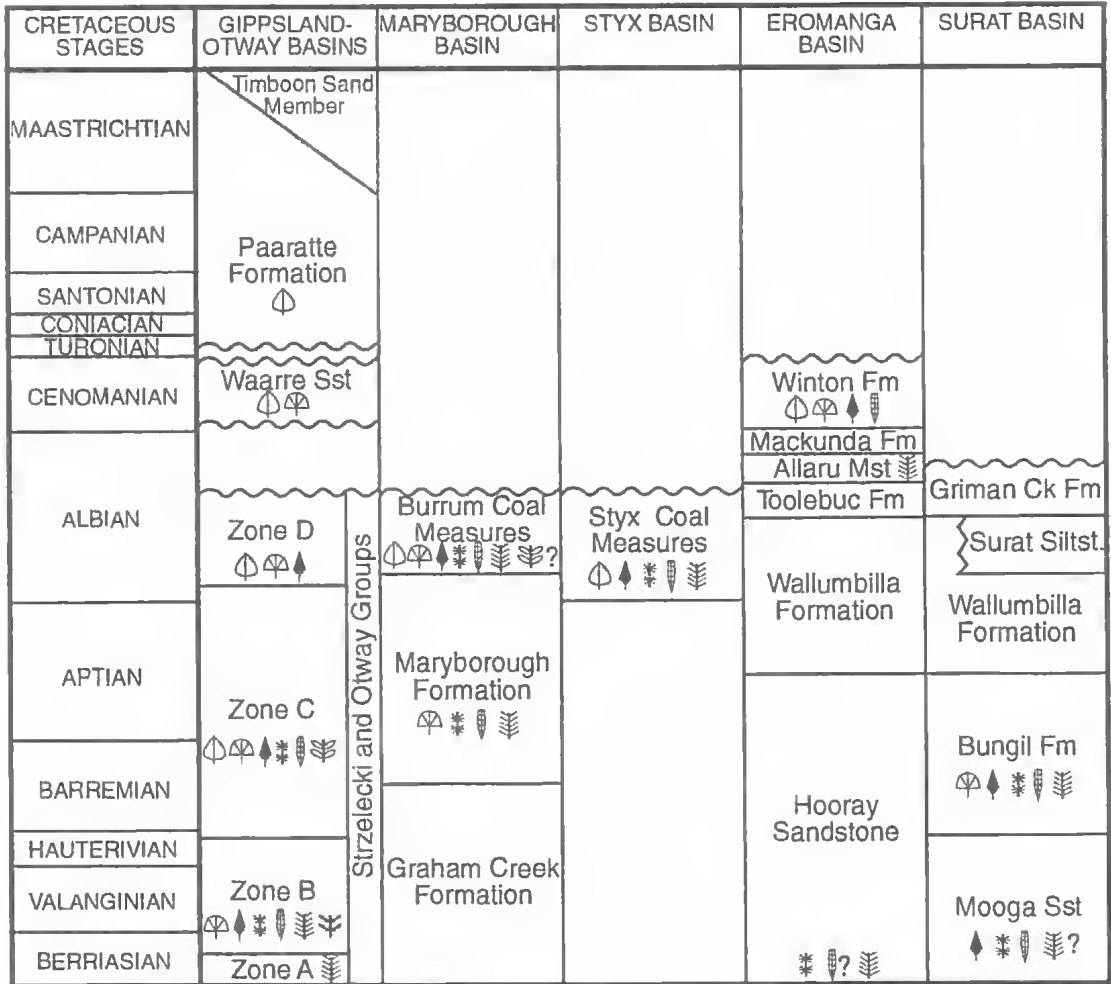
ern Hemisphere, but it appears that the same latitudinally diachronous pattern occurs (Drinnan & Crane, 1989). There is good evidence for considerable diversity in the Magnoliidae by the end of the Early Cretaceous, but quantitative analysis of Cretaceous palynofloras indicates that the mid-Cretaceous floristic transition to angiosperm-dominated floras mainly reflects the increasing diversity of non-magnoliid dicotyledons (Crane & Lidgard, 1989). These patterns imply that the transition from a pre-Cretaceous fern/gymnosperm vegetation to a flora dominated by angiosperms at the end of the Cretaceous has two components. The first is the "initial appearance" evidenced by monosulcate pollen representing the magnoliid dicot/monocot grade. The second component is "floristic domination" largely resulting from the diversification of triaperturate pollen diagnostic of the non-magnoliid dicot clade.

The Winton Formation is stratigraphically and floristically associated with the second component, the increasing diversity and dominance of non-magnoliid dicotyledons. All but one of the

angiosperm leaf taxa are of the simple hamamelid type, with probable fagaceous or betulaceous affinity. All have simple craspedodromous venation and, where higher order venation is preserved, it forms a well developed reticulum. The composition of the Winton angiosperm flora is very different to the well documented middle Cretaceous angiosperm floras of the Potomac Group on the Atlantic Coastal Plain of the United States, which form the basis of current hypotheses of angiosperm origin and diversification (Doyle & Hickey, 1976; Hickey & Doyle, 1977). The Winton flora does not contain any magnoliid leaves. Small "palaeoherb" leaves with unordered venation are characteristic of Potomac Group Zone I (Aptian) localities, peltate nelumbonaceous types are common in the Albian Subzone II-B,

and elliptical leaves of magnoliaceous/lauraceous affinity are prominent in the upper half of the Potomac sequence. The hamamelid component of the Potomac Group flora dominates Subzones II-B and III (Albian-Cenomanian) and consists largely of trilobed, palmately veined (*Araliopsoides*) and compound, pinnate (*Sapindopsis*) leaves that are of platanaceous and rosiid affinities (Crane et al., 1993; Upchurch et al., 1994).

Pole (1992) described a diverse collection of angiosperm leaves from several New Zealand localities ranging in age from Cenomanian to Maastrichtian. The hamamelid components are very like the leaves from the Winton Formation, but the New Zealand floras contain several extra forms, notably actinodromous, *Cinnamomum*-like, lauraceous leaves, several taxa with brochidodromous venation showing prominent secondary loops, and palmately veined leaves with prominent suprabasal secondaries. Daniel et al. (1990) summarised a New Zealand Cenomanian flora from the Clarence Series as having a range of magnoliid and hamamelid angiosperm



- ⊕ Angiosperms
- ⊕ Ginkgophytes
- ⬆ Phyllopteroides
- ⬆ Equisetaleans
- ⬆ Taeniopteris
- ⬆ Bennettitaleans
- ⬆ Thinnfeldia
- ⬆ Pachypteris

FIG. 26. Stratigraphic correlation of various Australian Cretaceous plant-bearing formations showing the distribution of selected plant groups.

leaves associated with a more typical Cretaceous conifer-“pteridosperm” assemblage including araucarians, several genera of Bennettiales, *Thinnfeldia*, Pentoxylales (*Taeniopteris*), cycads and *Ginkgo*; of these Bennettiales and *Thinnfeldia* are completely absent from the Winton gymnosperm assemblage, which consists predominantly of conifers.

Angiosperm leaves have been recorded from other mid-Cretaceous strata in eastern Australia (Fig. 26). Walkom (1919a) provided line draw-

ings of several pinnately veined leaves from the Albian Burrum and Styx Coal Measures, central Queensland. These floras contain a number of non-angiosperm taxa that are morphologically similar to Winton elements, including *Cladophlebis*, *Phyllopteroides*, *Sphenopteris*, *Microphyllopteris*, *Podozamites*, and especially *Ginkgo* and *Taeniopteris*. Bennettiales, which are absent in the Winton suites, are present in the Burrum and Styx floras. Medwell (1954b) illustrated two angiosperm leaves from an Albian

(latest Zone D) locality at Killara Bluff, western Victoria, and Douglas (1969) recorded a leaf and dispersed cuticle from similarly aged strata in subsurface drill core section (Yangery no. 1 bore). Zone D floras are well sampled from Victoria, and are dominated by *Elatocladus*, *Podozamites* and *Brachyphyllum* conifers, *Phyllopteroides*, and several finely dissected ferns. Bennettitales and *Taeniopteris* are absent, and *Ginkgo* is extremely uncommon. The Victorian Zone D floristic elements are not particularly like the similarly aged Burrum and Styx floras. The slightly younger Waarre Formation, which is known only from bore cores in western Victoria has yielded several small angiosperm leaves, and a species of *Ginkgo* similar to leaves found in the Winton, Burrum and Styx assemblages (Douglas, 1965).

Although the Winton Formation is known from only a small collection of localized floras, comparison with other floras of similar age provides an opportunity to propose a possible scenario of floristic transition through the Australian mid-Cretaceous. Valanginian to Aptian floras of southern Queensland and Victoria (Fig. 26) are essentially similar, and characterized by a predominance of conifers and linear *Taeniopteris* leaves with secondary veins perpendicular to the midvein. Together with a range of ferns such as *Cladophlebis* and *Sphenopteris*, they constitute an assemblage very similar to Jurassic strata of the Walloon Coal Measures (cf. Gould, 1974; McLoughlin & Drinnan, 1995); this is particularly evidenced by the perpetuation of early Mesozoic taxa such as *Palissyia* cones in the Neocomian and Aptian of Victoria (Parris et al., 1995). Small leaved Bennettitales such as *Ptilophyllum* and *Otozamites* are a prominent component of earliest Cretaceous floras that persist through the Albian in the Burrum and Styx Coal Measures in Queensland, but have already largely disappeared from Victorian floras by the Barremian. Bennettitales have not been recorded from the well collected Zones C and D of Victoria. The youngest Australian bennettitaleans appear to be represented in the late Albian Allaru Mudstone of central Queensland (Rozefelds, 1986). The apparent absence of Bennettitales in the Winton flora suggests that they have entirely disappeared from eastern Australia by the Cenomanian. This is somewhat different to New Zealand, where a considerable diversity is reported for the Clarence Series (Daniel et al., 1990) and they remain a component of some floras until as late as the early Senonian (McQueen, 1956).

Taeniopterid leaves also disappear earlier from Victorian floras. Linear leaves of the *Taeniopteris daintreei* type are a common and distinctive index fossil for the Victorian Zone C (Barremian-Aptian), but the Zone D (Albian) and younger sediments are devoid of taeniopterid leaves. Broader *Taeniopteris* leaves with angled secondary venation are present in Burrum and Styx floras, and persist in the Winton flora. Ginkgophytes have a disrupted record. In Victoria, deeply dissected leaves of *Ginkgo australls* are a common component of Zone C floras, but they are absent from adjacent Zones B and D. Smaller, more compact, and less dissected *Ginkgo* leaves persist in the Zone D and Waarre Formation floras (Douglas, 1965, 1970), and are more reminiscent of specimens from Burrum, Styx and Winton. Although the data is very sparse, they suggest that a widespread and comparatively uniform, eastern Australian, earliest Cretaceous flora (e.g., Maryborough Formation of Queensland and Zone C of Victoria) differentiated into different Albian floras in Victoria (Zone D) and Queensland (Burrum/Styx), and that it was these latter, central-eastern, Burrum/Styx type, floras that influenced Cenomanian floras of the Winton Formation in Queensland and possibly the Waarre Formation in Victoria.

The decline of bennettitaleans, pentoxylaleans, *Thinnfeldia*, *Pachypteris*, ginkgoaleans, and equisetaleans in the Australian flora appears to have occurred gradually through the Cretaceous and was matched by the appearance and steady increase in the diversity and abundance of angiosperms (Fig. 26). Eastern Australia remained in relatively high latitudes during the Cretaceous (Veevers et al., 1991) and although sea-levels varied considerably during that period (Frakes et al., 1987) it appears that no strong climatic changes affected the continent during that time although minor regional climate variation probably existed (Dettmann et al., 1992). Although rifting continued along Australia's western, southern, and southeastern margins and eastern Australia may have been broadly uplifted (Veevers et al., 1991), the continent did not experience significant mountain-building events in the mid-Cretaceous. The probable absence of a significant geographical or climatic cause for the disappearance of various (mostly deciduous) gymnosperm and herbaceous equisetalean groups might suggest that their demise was a direct response to competition from the emerging angiosperms. While this is difficult to confirm,

especially in the absence of a complete Late Cretaceous floral record, it is pertinent to note that several of these declining plant groups persisted later in the presumably more isolated New Zealand flora (McQueen, 1956; Daniel et al., 1990).

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